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THE PHYLOGENETIC RELATIONSHIPS OF SOFT-SHELLED TURTLES (FAMILY TRIONYCHIDAE)

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Phylogenetic analysis of 113 characters of the osteology of the 22 living species of trionychid turtles and representatives of all other living turtle families, provides abundant evidence on the relationships of soft-shelled turtles to other turtles and on the interrelationships within the family. These data suggest that the family Trionychidae shares a unique common ancestor with the Dermatemysidae, Kinosternidae, and Carettochelyidae, and that the Kinosternidae share a unique common ancestor with the Trionychidae and Carettochelyidae. Furthermore, it appears that the staurotypine kinosternids are most closely related to the Trionychidae and Carettochelyidae. Carettochelyids and trionychids share numerous unique features and clearly constitute a monophyletic group.

Within the Trionychidae, the subfamilies Cyclo-trionychidae and Trionychinae are recognized as monophyletic clades. Recognition of three cyclanorbine genera, Cycloderma, Cyclanorbis, and Lissemys, is warranted. Within the Trionychinae, four distinct clades are recognized. The Trionyx cartilagineus group includes Chitra indica and Pelochelys bibroni, on the basis of the unique location of the foramen posterior canalis carotici interni, and features of the trigeminal region. The North American group includes T. triunguis, T. euphraticus, T. swinhoei, T. ferox, T. spiniferus, and T. muticus, and can be recognized by the presence of eight or fewer neurals (first and second are fused), deeply emarginate prefrontals, and a large contribution by the parietal to the processus trocholearis oticum. The Indian group includes four species: T. gangeticus, T. hurum, T. leithii, and T. nigricans; all exhibit a free first neural, five plastral callosities, and intermediately extended epiplastra. Lastly, the T. steindachneri group, which includes T. steindachneri, T. sinensis, and T. subplanus, is diagnosed by a descending spine of the opisthotic that divides the fenestra postotica in most specimens.

Two equally parsimonious arrangements of the Trionychinae differ in the placement of the North American clade. In one, this clade is the sister group of the T. cartilagineus clade; in the other, it is the sister group of the T. steindachneri clade. In both, the Indian group is paraphyletic and gives rise to the T. steindachneri clade.

A revised classification of the family Trionychidae is provided. The use of 2 subfamilies, 6 tribes, and 14 genera is recommended. This expanded taxonomy will more completely reflect the hierarchical relationships that reflect recency of common ancestry as determined by the cladistic analyses.

Within recent years a fundamental revision of the systematic relationships of turtles has begun. This revision was precipitated by Gaffney (1975), who presented a reorganization of the Testudines using the cladistic method (as outlined in Gaffney, 1979a; Wiley, 1981). Other authors have followed Gaffney’s lead in applying this method to problems in chelonian systematics, resulting in a much clearer understanding of the phylogenetic relationships among turtle taxa. Concise hypotheses of the relationships within most families are now available (Proganochelyidae, Gaffney and Meeker, 1983; Chelidae, Gaffney, 1977; Baenidae, Gaffney, 1972; Meiolaniidae, Gaffney, 1983; Chelonioidea, Gaffney, 1976; Kinosternidae, Hutchison and Bramble, 1981; Trionychidae [shell only], Meylan, 1985; Emydidae, Hirayama, 1985; Testudinidae, Crumly, 1982, 1985) and are summarized by Gaffney (1984). The largest remaining family for which a complete cladistic study does not exist is that comprising the soft-shelled turtles, the Trionychidae.

This gap is significant, considering the large size, abundance, and great age of the family. The Trionychidae includes more than 250 named species (ca. 230 fossil and 22 extant) and occurs on every continent except Antarctica. It is a very old family, with definite representatives from the Cretaceous (Romer, 1956). Representation of this family in the fossil record is considerable, although difficult to document because few authors treat the fossils of this troublesome group. The best evidence of its ubiquity is reported by Hutchison (1982), who showed that the Trionychidae has the most continuous record of 11 reptile families examined from the Cenozoic of western North America.
Although authors do not agree on the relationships of trionychids to other turtles, I have never seen a single reference doubting the monophyly of the family. It is so distinctive that some authors have placed the family in a separate suborder equivalent to the Cryptodira and Pleurodira (Boulenger, 1889; Siebenrock, 1909; Bergounioux, 1932, 1955), an arrangement for which Loveridge and Williams (1957) found some support. Modern morphologists argue that this family is a group of aberrant cryptodires allied to the Carettochelyidae, Dermatemydidae, and Kinosternidae (McDowell, 1961; Albrecht, 1967; Zug, 1971; Gaffney, 1975, 1984). But others disagree, arguing that on the basis of karyology the Trionychidae, along with the Carettochelyidae, is the sister group of all other cryptodires (Bickham et al., 1983). On the basis of serological tests, Frair (1983) supported the placement of the family in its own suborder.

Among those workers willing to place the Trionychidae among the Cryptodira, there is difference of opinion as to which cryptodire families are the closest relatives of soft-shelled turtles. Since its discovery, Carettochelys Ramsay (1886) has been considered closely related to the Trionychidae, although some authors were confused by false reports of mesoplastra in this genus (Boulenger, 1889; Pritchard, 1967). Among the authors who have recognized close relationships between Carettochelys and the Trionychidae (Boulenger, 1889; Baur, 1890, 1891b; Waite, 1905; Siebenrock, 1902, 1913), some have recommended that superfamilial status be recognized (Trionychia, Hummel, 1929; Trionychoidae, Walther, 1922).

Several morphologists (Baur, 1891a; McDowell, 1961; Albrecht, 1967; Zug, 1971; and Gaffney, 1975, 1984) have allied the Trionychidae and Carettochelyidae with the Dermatemydidae and the Kinosternidae. Gaffney (1975) applied the name Trionychoida to this group. This enlarged concept of the Trionychoida is in clear conflict with the frequent association of the Kinosternidae with the Chelydridae and the inclusion of these two families in a clade with the Emydidae and Testudinidae. This latter arrangement was proposed by Williams (1950) and is based on the morphology of the cervical vertebrae and other osteological characters and has been followed by Romer (1956), Pritchard (1967, 1979a, 1979b), Mlynarski (1976), and others. Karyotypic data have recently been cited which partially support this arrangement (Bickham and Carr, 1983). It is obvious from these various arguments that the phylogenetic position of the family Trionychidae within the Testudines is still in question.

A narrower but equally urgent problem concerns the interrelationships within the family Trionychidae. The lack of resolution of relationships within the family is indicated by the current placement of nearly all species (ca. 235) in a single "wastebasket" genus, Trionyx. For more than 50 years since the major revision by Hummel (1929), there has been a strong tendency to synonymize trionychine genera (except Chitra and Pelochelys) with Trionyx (Bergounioux, 1955; Romer, 1956; Huene, 1956), with the result that 47 generic names are now considered synonyms (Smith and Smith, 1980). The apparent reason for this is not uniformity of morphology, but rather an absence of a complete and systematic interpretation of the characters. The large number of taxa and high intraspecific variability in the shape and degree of ossification of both the shell and skull make any study of trionychid relationships using a phenetic method extremely difficult. The most important recent studies are those of Loveridge and Williams (1957) and De Broin (1977).

On the basis of osteological characters, color pattern, and geography, Loveridge and Williams arrived at the arrangement redrawn as figure 1. The De Broin (1977) arrangement is based largely on characters of the shell and skull (especially the palate), but is given in insufficient detail to allow construction of a branching diagram. Both the Loveridge and Williams (1957) and De Broin (1977) arrangements contain features which appear in a cladistic analysis of the family based on shell morphology (Meylan, 1985).

Phylogenetic analysis provides a methodological breakthrough that has allowed elucidation of trionychid relationships. This method results in arrangements of taxa in hierarchies of internested natural groups. Because uniquely derived character states are used only from that point in the hierarchy beyond which they are shared by all taxa,
Recognition of the diagnostic features of monophyletic groups produces a strong hypothesis for the proper position of the Trionychidae among the Testudines and clarifies the interrelationships of its living species. In this work I have developed a hypothesis of cladistic relationships for the 22 Recent species of the family Trionychidae. The availability of large series of most living species and the completeness of Recent specimens has allowed a more complete character analysis than could be developed from fossils alone. A complete revision of the fossil members of the family lies beyond the scope of this study and will take many years to complete.

One of the most laudable aspects of phylogenetic analysis, which is absent from phenetic methods, is that it requires an observer to look beyond the taxa of immediate interest. Decisions about the polarity of character change in the ingroup (the Trionychidae) requires information from related forms. Therefore this study of the relationships of the members of a single family includes an investigation of interfamilial relationships and consequently has evolved into a study of representatives of the entire order. With its scope expanded by the requirements of phylogenetic methodology, this study has produced significant data on the distribution of character states among all turtles. These data are valuable in assessing the interfamilial relationships of trionychids.

The methodology employed also provides a means for identifying those characters which have states that appear to have been gained or lost independently, or which may have undergone reversal. These events, termed homoplasy, are the single most confounding feature in systematics. When systematic evaluations must be made from limited data sets, as in paleontology, it is important that characters subject to homoplasy are identified. Because most fossil Trionychidae have been described from shell material, an analysis of homoplasy in shell characters is critical to future work on the systematics of fossil forms.

The descriptive portions of this study focus entirely on characters significant in producing a phylogenetic arrangement for the ingroup. They are not meant as an exhaustive description of the osteology of the Trionychidae. Such a study has long been available (Ogushi, 1911).
The primary objectives of this project are to fill the largest remaining gap in our understanding of the phylogeny of living turtles by (1) determining the best placement of the Trionychidae within the Testudines; and (2) resolving relationships among the 22 extant trionychid species. In addition, this study will help provide a basis for future analysis of the relationships among the approximately 230 species known only from fossil material.

METHODS

THE PHYLOGENETIC METHOD

Systematics is not only a means of providing names for organisms and groups of organisms, but also a method by which we can infer and express the historical data of their descent. Biologists agree that all organisms have evolved by a single phylogenetic progression. The actual pedigree of taxa represents a succession of shared ancestries. Analysis of common ancestry can be a powerful explanatory tool for the distribution of traits of functional morphology (Lauder, 1982), ecology (Sears, 1984), physiology (McNab, 1978), and behavior (Meylan and Auffenberg, 1986). But the possibility that any features are a result of shared common ancestry rather than more proximal causes cannot be explored unless classification reflects this single phylogenetic progression. Consequently, it is critical for systematists to propose classifications which reflect shared common ancestries. The cladistic method is explicit in its reliance on shared derived characters, which are a function of the descent of species.

The phylogenetic method relies on the identification and use of shared derived characters to discover recency of common ancestry. Given that parallelism is the exception rather than the rule, any two taxa are more likely to have a shared trait because it was present in their common ancestor rather than because it appeared independently on two occasions. Thus the distribution of shared derived characters among taxa can be used to build a hierarchical ranking of recency of common ancestry.

Developing this hierarchical ranking requires (1) identification of characters with appropriately distributed character states; (2) identification of primitive versus derived states for the characters; and (3) a system for the formulation of hypotheses of hierarchical relationship using the shared derived character data in the most efficient (parsimonious) manner.

CHARACTERS AND CHARACTER STATES

The systematics of soft-shelled turtles has been based almost exclusively on skeletal morphology (see for example Baur, 1893; Siebenrock, 1902; Hummel, 1929; Stejneger, 1944; Loveridge and Williams, 1957; De Broin, 1977). Characters of the external soft anatomy are of little use, and few studies have employed them. The exceptions are the use of color pattern (Loveridge and Williams, 1957; Webb, 1962) and the presence of femoral and caudal valves in the Cyclanorbinae (most studies). For this reason, the character survey in the present study was restricted to skeletal morphology. A secondary advantage of this emphasis is future direct application of this study to the interpretation of the relationships of fossil trionychid species.

Character of two types were sought: those uniform within the family but varying among higher taxa outside the family; and those varying among different groups of trionychid species. The former (interfamilial characters) provide a data set for hypotheses on the placement of trionychids within the Testudines. The latter (intrafamilial characters) provide a basis for developing phylogenetic hypotheses for species within the family Trionychidae.

Variation in a given character is treated as states of that character. Many of the characters used have only two states, such as presence or absence of a given bone, structure, or contact. Other characters include three or more discrete states or continuous variation. Multistate and continuous characters pose two methodological problems. First, for purposes of analysis it is necessary to divide a
CONTINUOUSLY VARYING CHARACTER INTO A NUMBER OF DISCRETE STATES. SECONDLY, IT HAS BEEN PROPOSED (GAFFNEY, 1979A, PERSONAL COMM.) THAT RECOGNITION OF INTERMEDIATE STATES REQUIRES AD HOC HYPOTHESES THAT EVOLUTION HAS OCCURRED IN CERTAIN WAYS, AND THEREFORE MULTISTATE CHARACTERS SHOULD BE AVOIDED.

INFORMATION CONTAINED IN MULTISTATE CHARACTERS, OR MORPHOCLINES, IS EXTREMELY USEFUL FOR UNDERSTANDING THE HISTORY OF DESCENT OF ANY GROUP (MASLIN, 1952) AND HAS BEEN CRITICAL IN FORMULATING A HYPOTHESIS OF RELATIONSHIPS FOR TRIONYCHIDS BASED ON THE SHELL ALONE (MEYLAN, 1985). THE MULTISTATE CHARACTERS THAT HAVE BEEN USED IN THE PRESENT STUDY ARE OF THREE TYPES: (1) CONTINUOUS CHARACTERS OF SHAPE, SIZE, RELATIVE POSITION, ETC., FOR WHICH STATES HAVE BEEN DETERMINED BY THE OCCURRENCE OF NATURAL BREAKS ALONG A CONTINUUM; (2) DISCRETE CHARACTERS OF A MERISTIC NATURE FOR WHICH MORE THAN TWO POSSIBLE STATES EXIST; AND (3) TWO-STATE CHARACTERS IN WHICH BOTH STATES FREQUENTLY OCCUR IN THE SAME SPECIES, REQUIRING THE RECOGNITION OF THAT THIRD, INTERMEDIATE CONDITION. I SUBMIT THAT IN ALL OF THESE CASES, AS FOR TWO-STATE CHARACTERS, ONLY A HYPOTHESIS OF CHARACTER POLARITY IS NECESSARY. BY INVOKING THE PRINCIPLE OF Parsimony WE CAN SUGGEST THAT THE DEGREE OF CHANGE REQUIRED TO ARRIVE AT A GIVEN STATE SHOULD BE MINIMIZED, JUST AS THE NUMBER OF POSTULATED CHANGES IN A CLADE ARE ORDINARILY MINIMIZED BY PHYLLOGENETIC SYSTEMATICS. FOR EXAMPLE, WE COULD PROPOSE THAT EXTREME REDUCTION OF PERIPHERAL BONES IN LISSEMY occurs independently of complete loss of peripheral bones in all other trionychids (two steps) or that reduction in LISSEMY is followed by complete loss in other trionychids (also two steps). BUT THESE TWO TWO-STEP CHANGES ARE NOT EQUIVALENT. ONE REQUIRES TWO COMPLETE CHANGES FROM AN APPARENTLY VERY FIXED PRIMITIVE CONDITION (LOSS OF PERIPHERAL BONES OCCURS OTHERWISE ONLY IN DERMOCHELYS); THE OTHER REQUIRES A SINGLE DIVERGENCE FROM THE PRIMITIVE CONDITION WHICH IS SUBSEQUENTLY ELABORATED.

MULTISTATE DISCRETE CHARACTERS (E.G., NUMBER OF PERIPHERALS OR NEURALS) PRESENT LITTLE PROBLEM FOR THE RECOGNITION OF DIFFERENT CHARACTER STATES. CONTINUOUS CHARACTERS OF RELATIVE SIZE MUST BE DIVIDED INTO STATES BY SOME ARTIFICIAL BUT OBJECTIVE MEANS. AS IN OTHER STUDIES (MARX AND RABB, 1972; DREWES, 1984), I HAVE DIVIDED CONTINUOUS CHARACTERS BY PLOTTING THE AVERAGE VALUES FOR TERMINAL TAXA ALONG A CONTINUUM, AND employing natural breaks in distribution as evidence of various character states (see fig. 2, for example). IF NO NATURAL BREAKS IN DISTRIBUTION OCCURRED, THE CHARACTER WAS DISCARDED.
The characters employed in this study are given equal weight. Certain authors, most notably Hecht and Edwards (1977), have argued that some types of characters, for example those involving loss, should be given little weight. In this study characters are weighted only in the sense that they have been included or discarded, depending on the distribution of variation. I disagree with the concept of a priori character weighting in general, and in particular, I do not accept the supposition of Hecht and Edwards that characters involving loss are necessarily simple and subject to homoplasy, and therefore should be given low weight. The loss of a major structure such as the peripheral bones in turtles or the neural spine in snake vertebrae (a character of lowest value in the Hecht and Edwards' scheme) can occur only when a complex structural alternative (a character of highest value in the Hecht and Edwards' scheme) is available. The losses mentioned above require the development of strong and deeply sutured rib heads in the case of certain trionychoids, and relocation of numerous muscles that originate or insert on the neural spine in snakes. This may explain why complete loss of each of these features has apparently occurred only once. In both instances, loss is the immediately apparent result of a complex evolutionary event, and therefore should not be discounted.

There are two reasons for the inclusion of a maximum number of characters in this analysis. First, such inclusiveness is necessary to provide results that will be of greatest value to paleontology. Paleontologists are often faced with solving systematic problems on the basis of incomplete material. By increasing the number of characters, there is an increased likelihood that characters present in any given fossil will have been studied. The second reason is to provide separate data sets to test the monophyly of problematic groups and detect homoplastic character states.

Because there are 113 characters discussed in this paper, some means of assisting the reader is required. Therefore, the characters are numbered. Characters 1–30 pertain to the shell, 31–78 pertain to the skull, and 78–113 pertain to the visceral skeleton and nonshell postcrania.

**Character Polarity**

Once the states of a given character have been recognized, it is essential to identify the primitive and derived extremes, or character polarity. Numerous criteria for determining the polarity of character transformations have been offered in the literature. The most often treated are outgroup comparison, commonality, evidence from the fossil record, evidence from embryology, and correlation of character states (Kluge and Farris, 1969; Marx and Rabb, 1972; Wiley, 1981). I follow Gaffney (1979a), Watrous and Wheeler (1981), and Wiley (1981) in relying on outgroup comparison as the best criterion for character polarity decisions. This criterion has been discussed at some length in recent systematic literature and methods have been outlined for making the most efficient use of outgroups when they are well established (global parsimony, Maddison et al., 1984), or when a number of outgroups could be the sister taxon to the ingroup (outgroup substitution, Donoghue and Cantino, 1984).

In this study I have employed data from all families of turtles and the arrangement of Gaffney (1984) to make use of the concept of global parsimony. That is to say, the outgroup for the Trionychidae is all other turtles. Decisions concerning polarity of characters within this family are most directly affected by the distribution of states within the Trionychoidea. The concept of the Trionychoidea is based on characters polarized at a higher level of universality.

**Formulation of Phylogenetic Hypotheses**

In my provisional arrangement of the Recent species of the Trionychidae based on 16 characters of shell morphology (Meylan, 1983), I conducted the search for the most parsimonious cladogram (that requiring the fewest evolutionary steps) by hand. As additional data have been assembled for this study I have partitioned them into three sets (shell, skull, and visceral skeleton plus nonshell postcrania). As each of these data sets became very large, it became necessary to employ a computer program to generate cladograms. I used Phylogenetic Analysis Us-
Using Parsimony (PAUP, version 2.3, 1984) by D. Swofford, which was made available through the Northeast Regional Data Center at the University of Florida.

PAUP emphasizes simple unrestricted parsimony procedures (Swofford, 1984). Its author finds that there is close correspondence between results obtained by hand and those generated via PAUP. One advantage in addition to the time-saving capabilities of PAUP is the MULPARS option. This option results in a listing of all “most parsimonious” trees. It seems certain that when working by hand one is unlikely to discover all such trees. The ability of the program to handle missing values improved its utility for use in the current project.

I have employed PAUP to formulate the most parsimonious hypothesis of relationship for the species within the family Trionychidae that can be derived from each of the three independent sets of osteological data. These are (1) 22 characters of the shell (an expanded version of Meylan, 1985); (2) 23 characters of the skull; and (3) 13 characters of the lower jaw and postcrania (exclusive of the shell). Additionally, an analysis of the three data sets combined was performed.

**Comparison of Fundamental Hypotheses and Formulation of a General Hypothesis**

Following the development of cladograms from the three separate data sets, it was desirable to formulate a single general cladogram from them and to compare the utility of various characters, especially those of the shell, in the formulation of this general hypothesis. Two methods, analysis of the three data sets in combination and a stepwise consideration of compatible characters, have been used for this procedure. Neither the Nelson (1979) method nor the similar Adams (1972) method produced a single, well-resolved cladogram of trionychid relationships.

**Basic Taxa**

The species of living trionychid turtles recognized for this study are essentially those listed by Wermuth and Mertens (1961). The only differences are the use of the name *Trionyx swinhoei* for the large and colorful Chinese species which these authors had relegated to the synonymy of *Trionyx sinensis* (De Broin, 1977; Meylan and Webb, 1987) and the relegation of *Trionyx ater* to subspecific level within *T. spiniferus* (Smith and Smith, 1980). The 22 species used are the same as those employed in Loveridge and Williams (1957).

Two species recognized since the publication of Wermuth and Mertens (1961) have been deemed insufficiently distinct to be used in the current study. On the basis of the absence of integration between *Lissemys scutata* and *L. punctata*, Webb (1982) proposed that the former be considered a full species rather than a subspecies of *L. punctata* (Annanadle, 1912; Deraniyagala, 1939; Wermuth and Mertens, 1961). The primary morphological differences between the two are the configuration of the peripherals and the early development of plastral callosities in *L. scutata*. All superficial dermal callosities are highly variable within trionychid species, and thus additional, less variable features should be found to corroborate the validity of *L. scutata* before it is considered a distinct species. If *L. scutata* is distinct, there is little doubt that *L. punctata* is its closest relative.

The name *Trionyx nakornsrithammajensis* was proposed for a “rare softshell” from Thailand (Wirot, 1979). Judging from the color pattern of the specimen in the figure included with the description, this name applies to *Trionyx cartilagineus*.

**Terminology**

**Taxonomy**

Existing generic assignments are used for trionychids throughout the results and discussion sections of this paper. However, since the generic name *Trionyx* is currently used with about three-fourths of the species, little information is conveyed by the use of generic names. Therefore, specific epithets are used alone in figures and tables throughout.

Certain collective terms are used provisionally for groups of trionychid species throughout the text. They are used for groups which have been suggested to be monophyletic by more than one author. The Cyclanorbinae (Cyclanorbidae of Deraniyagala, 1939; or Lissemydinae, of Williams, 1950)
includes Cyclanorbis elegans, Cyclanorbis senegalensis, Cycloderma aurbyi, Cycloderma frenatum, and Lissemys punctata. These species are considered to constitute a natural group in treatments by Deraniyagala (1939), Loveridge and Williams (1957), and Meylan (1985). The sister group of the Cyclanorbinae is the Trionychinae, which includes all non-cyclanorbine members of the family. There is good evidence that the Trionychinae is a monophyletic group (Meylan, 1985). It has been recognized as such by Deraniyagala (1939), and Loveridge and Williams (1957). Within the Trionychinae two species groups have been treated as natural in all recent accounts: the four species of the Indian subcontinent (Trionyx gangeticus, T. leithii, T. hurum, and T. nigricans); and the three North American forms (T. ferox, T. muticus, and T. spiniferus) (Loveridge and Williams, 1957; De Broin, 1977; Meylan, 1985).

Names of familial and higher taxa of the Testudines are those suggested by Gaffney (1984). Monophyly of these taxa is not reexamined except for the superfamily Trionychoidea and its member families. The suffixes -oidea for superfamilies, -idae for families, and -inae for subfamilies are used consistently throughout the Testudines.

RESULTS

VARIATION IN SHELL MORPHOLOGY

Thirty characters of the carapace and plastron have been determined to be useful for establishing inter- and/or intrafamilial relationships of trionychid turtles (table 1). They pertain to carapace size and shape, the nuchal region, the neural series, the shell periphery, posterior end of the carapace, and the plastron. Because of the unique nature of the shell of trionychids few of these characters are useful in testing proposed interfamilial relationships.

All character polarities discussed in this section are based on outgroup comparisons. It is therefore important that doubts about the homology of the shell of trionychids to that of other turtles be considered. Zangerl (1969) contended that the external bony layer in the Trionychidae and Dermochelyidae is composed of epithelial ossifications of more superficial origin than the dermal ossifications considered to form the shell in other turtles. This implies that the superficial layer of the shells of members of these two families are not strictly homologous to the same layer in other turtles. The existence of a nonhomologous superficial layer seems quite possible for Dermochelys in which there is total independence of the superficial bone and the deeper dermal elements of the shell (i.e., the ribs and neural spines of vertebrae). In cross section these “epithelial bones,” which make up the superficial bony mosaic, lack dense layers on the external and internal surfaces (fig. 3, bottom). Thus they do not fit Zangerl’s (1969) description of turtle shell bone of typ-
## Table 1

### Shell Characters and Character States Used for Resolving Phylogenetic Relationships of Recent Trionychid Turtles.

For each character the most primitive state is number 1

<table>
<thead>
<tr>
<th>Characters</th>
<th>Character states</th>
</tr>
</thead>
</table>
| 1. width/length of nuchal bone | 1. less than 2  
2. greater than 2  
3. greater than 3  
4. greater than 4 |
| 2. anterior and posterior costiform processes of nuchal bone united | 1. no  
2. yes |
| 3. position of anterior edge of first body vertebra relative to nuchal bone | 1. posterior edge of nuchal  
2. middle of nuchal  
3. anterior edge of nuchal |
| 4. first and second neurals fused | 1. no  
2. yes |
| 5. total number of peripherals | 1. 22  
2. 20  
3. 14-18  
4. 0 |
| 6. peripherals sutured to pleurals | 1. yes  
2. no |
| 7. prenuchal bone | 1. absent  
2. present |
| 8. size of eighth pleurals | 1. large  
2. reduced or absent  
3. seven  
4. five  
5. four  
6. two  
7. none  
8. nine |
| 9. number of plastral callosities | 1. open throughout life  
2. always at same neural  
3. always at adjacent neurals  
4. highly variable |
| 10. hyoplastra and hypo-xiphiplastra fuse just after hatching | 1. yes  
2. no |
| 11. hyoplastra and hypo-xiphiplastra fuse in adults | 1. absent  
2. present |
| 12. fusion of xiphiplastra | 1. xiphiplastra lateral to hyoplastra  
2. hypo-xiphiplastra lateral to xiphiplastra |
| 13. hypo-xiphiplastral union | 1. short  
2. intermediate  
3. long |
| 14. number of neurals (fused 1 and 2 counted as 2) | 1. anterioposteriorly elongate or round  
2. “boomerang-shaped” |
| 15. variability in position of neural reversal | 1. at neural eight  
2. at neural seven  
3. at neural six or seven  
4. at neural six  
5. at neural four, five, or six |
| 16. pleurals which meet at midline | 1. eighth only  
2. seventh and eighth or eighth only  
3. sixth, seventh, and eighth or seventh and eighth  
4. more than sixth, seventh, and eighth |
| 17. point of reversal of orientation of neurals | 1. closed at hatching  
2. closed in large adults only  
3. open throughout life |
| 18. suprascapular fontanelles | 1. J-shaped  
2. I-shaped |
| 19. epiplastron shape | 1. at neural eight  
2. at neural seven  
3. at neural six or seven  
4. at neural six  
5. at neural four, five, or six |
| 20. length epiplastron anterior to entoplastron contact | 1. present  
2. absent |
| 21. depressions on eighth pleurals for contact of ilia | 1. closed at hatching  
2. closed in large adults only  
3. open throughout life |
| 22. shape of entoplastron | 1. at neural eight  
2. at neural seven  
3. at neural six or seven  
4. at neural six  
5. at neural four, five, or six |
| 23. bridge length | 1. long  
2. short |
| 24. largest adult size 200 mm or less (disc length) | 1. no  
2. yes |
| 25. carapace margin straight to concave posterolaterally | 1. at neural eight  
2. at neural seven  
3. at neural six or seven  
4. at neural six  
5. at neural four, five, or six |
| 26. plastral buttresses reach across peripherals to contact pleurals | 1. both axillary and inguinal  
2. axillary only  
3. neither |
| 27. carapace sutured to plastron all across bridge | 1. yes  
2. no |
| 28. rib heads strongly sutured to vertebral centra | 1. yes  
2. no |
| 29. sexual dimorphism in disc length | 1. yes  
2. no |
| 30. shell sculptured and lacking epidermal scutes | 1. yes  
2. no |
Fig. 3. Cross sections of single pleural elements of three cryptodiran turtles. Top, *Chrysemys picta* (UF 40615); middle, *Trionyx ferox* (UF 54212); bottom, *Dermochelys coriacea* (UF 37557).

nal dermal origin. The case is less clear for the most superficial bony layer in the Trionychidae. In members of this family, as in other turtles, there is complete correspondence between superficial bony elements and underlying deep dermal elements of the carapace. Furthermore, cross sections of either carapacial or plastral elements of trionychids reveal the presence of a spongy middle region with compact lamellar layers on either side (fig. 3 top, middle). This agrees with Zangerl's own description of typical dermal shell bone and fits Suzuki's (1963) description of the results of development of dermal shell bone in *Pseudemys scripta*. Zangerl's (1939) original argument for an episthecal origin of the superficial bone in trionychids is based on its delayed development rather than on its site of origin. The late development of the superficial layer does not have any clear bearing on the homology of its origin, and must yield to the physical evidence that, in cross section, trionychid shell elements do not differ significantly from other sectioned chelonian shells which are considered to be of normal dermal origin. Thus, unless other evidence can be provided, the superficial elements of trionychid shells may be regarded as homologous to those of other turtles.

**CARAPACE SIZE AND SHAPE**

Even the smallest fragment of trionychid shell is immediately recognizable by its characteristic sculpturing. This sculpturing is never divided by scute sulci because scute sulci and the epidermal scutes they delineate, which are present on the shells of most other turtles, are always absent in trionychids. The only other living turtle which has a sculptured shell and lacks epidermal scutes is *Carettochelys*. The absence of epidermal scutes is considered to be a derived condition (character 30, table 8).

Recent trionychids are, for the most part, large turtles and many species approach one meter in total carapace length. The carapace consists of a bony disc with cartilaginous margins. In discussions of osteological material, including this one, it is the bony disc length rather than total carapace length which is used as an index of total size. The largest species of trionychids have bony discs over 500 mm in length; most reach disc lengths of 300 mm (table 2). The exceptions are few, and these are usually 200 mm or less in disc length.

Five species of *Trionyx* are small (under 200 mm disc length): *Trionyx muticus, T.*
TABLE 2

Maximum Size of Recent Trionychids (Character 24)

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<th>Species</th>
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<tr>
<td>bibroni</td>
<td>BMNH 80.4.25.6</td>
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<td>ZSM 832/1920</td>
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<td>elegans</td>
<td>NMW 1437</td>
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<td>cited in Siebenrock, 1913</td>
<td>282</td>
</tr>
<tr>
<td>ferox</td>
<td>UF 45341a*</td>
<td>371</td>
</tr>
<tr>
<td>formosus</td>
<td>cited in Annandale, 1912</td>
<td>274</td>
</tr>
<tr>
<td>frenatum</td>
<td>BMNH (Type of Aspidochelys livingstoni)</td>
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<tr>
<td>gangeticus</td>
<td>cited in Annandale, 1912</td>
<td>485</td>
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<tr>
<td>hurum</td>
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<td>leithii</td>
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<td>124</td>
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<tr>
<td>nigricans</td>
<td>cited in Annandale, 1912</td>
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</tr>
<tr>
<td>punctata</td>
<td>cited in Deraniyagala, 1939</td>
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<tr>
<td>subplanus</td>
<td>calculated from skull ca. 250</td>
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<tr>
<td>swinhoei</td>
<td>calculated from fig. 1A, Heude, 1880</td>
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</tr>
<tr>
<td>riunguis</td>
<td>KNM-VP-ER-8123</td>
<td>410</td>
</tr>
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</table>

* Allen (1982) reported an apparently larger Trionyx ferox.

Among other trionychoids, small size is common only in the Kinosternidae. Most known species of the Dermatemyidae and Carettochelyidae reach bony carapace lengths of 400–500 mm. Among the Kinosternidae the genus Staurotypus reaches adult sizes close to those of Dermatemys and Carettochelys; whereas Claudius, Kinosternon, and Sternotherus are smaller, usually under 200 mm. It seems likely that reduction in total size is a derived condition common to the Kinosterninae and that similar diminution occurred independently in one or more groups within the Trionychidae. Thus, small carapace size is considered to be a derived condition among trionychids (character 24, table 3).

Sexual dimorphism in total size is well known for turtles. In certain forms the male is larger and in others the female is larger. The latter occurs most frequently among aquatic emydids but also occurs in some trionychids. Webb (1962) provides data which indicate that all three North American forms are sexually dimorphic in size. This has not been shown for any Old World forms with the possible exception of Chitra indica (Wirot, 1979). Because of apparent absence among other trionychoids, sexual dimorphism, in which the female is larger, can be considered a derived feature within the Trionychidae (character 28, table 3).

The carapace of trionychids is unique among the Testudines in having a flexible margin. This margin varies in extent and thus in flexibility. In one species (Lissemys punctata) it makes up less than 10 percent of the total carapace length and contains bony elements which are most likely homologous to the peripherals of other turtles (fig. 4A; see discussion of character 5 under section on shell periphery). In other forms the cartilaginous margin makes up almost one-half of the carapace length (fig. 4B) and the bony disc is thus quite reduced.

There can be little doubt that reduction of the bony disc relative to the total carapace is a derived condition, as it occurs only within this family. However, variation in this condition among trionychid species shows no natural breaks and I have not been able to convert this continuous variable into a discrete one. It should be pointed out, however,
that cyclanorbines consistently have relatively larger discs than trionychines and in this respect they represent the more primitive condition.

Elsewhere (Meylan, 1985) I have suggested that the shell outline of Cycloderma frenalum is unique in having a sharply tapering rear half of the carapace with straight-to-concave posterolateral edges (compare fig. 4A to figs. 4B, 5A, and 5B). After examination of numerous carapaces of Cycloderma aubryi and Lissemys punctata, it is apparent that these species share the unique carapacial outline noted above. Other trionychids, like most other testudines, have round-to-oval shells that are convex posterolaterally (character 25, table 3).

**NUCHAL REGION**

Dalrymple (1979) provides an excellent discussion of the role of the cervicodorsal joint in trionychids in allowing the retraction of a long neck into a small space. In order to accommodate such modification of this joint, the entire anterior portion of the trionychid carapace must have been extensively remodeled. In most cryptodires, the first thoracic vertebra is directly ventral to the first neural bone of the carapace (fig. 6A) and is firmly sutured to it. It is loosely jointed to the carapace and usually more anteriorly located in trionychids (fig. 6B–D). In Lissemys and Cycloderma, the first thoracic vertebra lies directly below the “preneural” to which it is weakly sutured, suggesting that the “preneural” is actually a first neural (see also Baur, 1893; Hay, 1908; Carpenter, 1981). The nuchals of Lissemys and Cycloderma are also the longest (relative to their width) among the trionychids (compare fig. 4A to figs. 4B, 5A, and 5B). Separate anterior and posterior costiform processes can be recognized (fig. 6B). Grooves for passage of the postzygapophyses of the eighth cervical vertebra are present on either side of the midline at the

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### TABLE 3

Modal Character States for Shell Characters of the Recent Trionychidae Used in Analysis of Intrafamilial Relationships

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<th>Characters</th>
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<td>triongus</td>
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</table>

* For descriptions of the characters and character states see table 1.
base of the posterior costiform process. This combination of features places a well-fixed first thoracic vertebra well back from the edge of the carapace (fig. 6B). Among trionychids the condition in Lissemys and Cycloderma most closely approaches that seen in other cryptodires. Further derived conditions include less contact between the first thoracic vertebra and the first neural and more posterior placement of the nuchal such that it lies above the first thoracic vertebra.

An advanced condition of the nuchal region appears in Cyclanorbis senegalensis, in which the length of the nuchal bone is reduced, bringing the first thoracic vertebra closer to the anterior edge of the carapace. The anterior and posterior costiform processes of the nuchal are not clearly separate (as in figs. 6C, D), but the first neural (pre-neural) is still distinct from the second (as in figs. 4A and 5B). A similar condition is found in Cyclanorbis elegans and in Trionyx gangeticus, T. leithii, T. nigricans, and T. hurum.

Fusion of the first and second neurals occurs only when the first thoracic vertebra is free of overlying neurals due to reduction of the neural arch of the vertebra. It is present in all Chitra, Pelochelys, and Recent Trionyx other than the Indian forms: T. hurum, T. leithii, T. nigricans, and T. gangeticus. Up to about 10 percent of certain Trionyx species (T. ferox, T. formosus, T. triunguis) show separate first and second neurals.

The extreme of development in this suite of characters is found in Chitra (fig. 6D). In C. indica, prezygapophyses of the first body vertebra are immediately adjacent to the anterior rim of the carapace, and the nuchal is reduced to a narrow sliver of bone. Very narrow costiform processes occur on the anterior margin, and depressions which allow passage of the postzygapophyses of the eighth cervical are present just inside the rim of the carapace. In Chitra there is also a new pair of processes at the posterior edge of the nuchal. They can be distinguished from the posterior pair in Cycloderma and Lissemys by their position well posterior to depressions for passage of the postzygapophyses of the eighth cervical.

Variation in the nuchal region has been analyzed through the use of four characters (tables 1, 3). The primitive condition for nuchal shape (character 1) is that most similar to those of other turtles, that is, length equal to width or nearly so. Costiform processes (character 2) are not present in adult Caret-
MEYLAN: TRIONYCHIDAE

Fig. 5. Dorsal views of the carapace of two trionychid turtles. A. Trionyx ferox (AMNH 129737); B. Trionyx hurum (BMNH 86.8.22.2).

tochelys, but in some juveniles of the related genus Anosteira, there are two pairs (Bramble, personal commun.). In other trionychoids (Kinosternidae and Dermatemydidae) there is one pair in adults. But in newly hatched Dermatemys (BMNH 1984.1291) there are, in fact, two pairs. A cleared and stained hatchling Sternotherus minor and a skeletonized Kinosternon flavescens in the UF collection also have indications of paired processes anterior to a well-defined pair of costiform processes. Thus it seems likely that two pairs are present early in the ontogeny of all trionychoids. In the Dermatemydidae and Kinosternidae the anterior of the two pairs disappears with age while in the Trionychidae the two pairs occur separately in some forms (Lissemyx punctata and both species of Cycloderma) and appear to be united in all others. Because this condition is probably present early in the ontogeny of all trionychoids, the possession of two pairs of costiform processes is considered primitive for trionychids.

Most cryptodires have the first thoracic vertebra at the posterior edge of the nuchal. As a result of apparent foreshortening of the nuchal in trionychids, the anterior edge of the shell comes to lie closer to the first thoracic vertebra. Close proximity of the anteriormost thoracic vertebra to the margin of the carapace is considered derived (character 3, table 3).

The trionychid “preneural” is here considered to be the first neural (see also Hasan, 1941). As suggested by Webb (1962) and Gaffney (1979c), fusion of the first neural to the second neural must be a derived character state (character 4). No nontrionychid member of the Trionychoidea always has two neurals between the first pleurals, but there are two in some Carettochelys (BMNH 1903.4.10.1). Furthermore, there are two thoracic vertebrae between the first pleurals of all trionychids. In T. ferox two neurals form (one on each of the first two thoracic vertebrae) and then fuse into a single element (Carpenter, 1981; present study).

The carapace of adult turtles is ordinarily a solid bony structure without openings or fontanelles. Peripheral fontanelles are not uncommon; they occur in juveniles of all cryptodires and are retained in some adult chelydrids, cheloniids, and trionychids. In trionychids, peripheral fontanelles are difficult to visualize because the peripheral bones
are lacking. Fontanelles closer to the midline of the carapace are much less common. They occur above the ilia in very old individuals of some testudinoids (e.g., Terrapene, Cuora, Gopherus, Homopus) and some Kinosternon, and above the scapulae (=suprascapular fontanelles) in certain trionychids and at least one testudinid, Homopus.

Suprascapular fontanelles are probably present early in the development of all trionychids. They are closed at hatching in some forms (Lissemys punctata) but remain open

Fig. 6. Internal views of the carapace of four eucryptodiran turtles. A. Trachemys scripta (AMNH 111961); B. Lissemys punctata (UF 56017); C. Trionyx ferox (AMNH 129737); D. Chitra indica (MCZ 29487). Surfaces for ilial articulation are stippled.
Suprascapular Fontanelles (Character 18) in the Carapace of Recent Trionychids

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<th>Species</th>
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<th>C</th>
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</table>

- Disc length (mm) for the largest specimens with fontanelles (A), smallest specimen without fontanelles (B), and largest specimen examined for fontanelles (C) are given for each species.

Throughout life in others (Trionyx subplanus, T. spiniferus [except some old males], T. muticus, and T. steindachneri). In most trionychids suprascapular fontanelles close up at some point between hatching and the attainment of adult size (Table 4). However, insufficient data on the timing of closure in most species prevents the use of this character. Early loss of the fontanelles is likely the primitive condition and lifelong retention derived.

The Neural Series

The above argument suggests that the trionychid "preneural" of many authors is the first neural. Thus the most complete neural series in trionychids includes nine elements between the nuchal and eighth pleurals. The normal pattern in cryptodires is a continuous series of neurals from the nuchal to the suprapygal, with uniform orientation. All trionychids lack a suprapygal, and the eighth pleurals meet at the midline (except in Trionyx subplanus). The most complete series of nine neurals, with all or the majority (numbers 2–7) hexagonal and uniformly facing posteriorly (see below), is likely to be the most primitive condition among living trionychids.

Modification of the presumed primitive condition results from four apparently independent changes: (1) the fusion of the first and second neural (treated above, character 4), (2) interruption of the neural series by pleurals meeting at the midline (character 16), (3) variation in the number of neurals expressed on the dorsal surface of the carapace (character 14, table 5), and (4) variation in the location at which orientation of the neurals reverses (character 17, table 6). There are also interspecific differences in the amount of variability in the point of neural reversal (character 15). That is to say, in some species...
### Location of Reversal in Neural Orientation in Recent Trionychids

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*Location of the most posterior reversal is given as a frequency of occurrence at or between neurals. Values which do not sum to 1.0 are due to individuals with no neural reversal (see table 7). Trionyx formosus, T. nigricans, and T. swinhoei are excluded due to insufficient sample sizes; in Cyclanorbis senegalensis the neural series is too fragmented to allow the detection of reversals.*

The location of reversal is always at the same neural; in others, neural reversal occurs only at either of two adjacent neurals; and in still others, it may occur anywhere along the neural series. Interruption of the neural series by pleurals meeting at the midline is not common among cryptodires. Most species have a neural series which is uninterrupted from the nuchal to the suprapygal. In dermatemydids and kinosternids, posterior pleurals may meet on the midline but in this case the posteriormost neurals usually do not appear and so they cannot be isolated from the anterior portion of the series. In *Carettochelys* pleurals often meet along the midline, isolating sections of the neural series. The neurals of *Carettochelys* are extremely narrow and thus appear to be less generalized than those of trionychids. Relying on global parsimony in establishing polarity in this case, I must consider the absence of pleural interruption of the neural series primitive for the Trionychidae.

Actually, interruption of the neural series is rare in trionychids. The last neural is isolated from the rest of the neural series in occasional specimens of *Lissemys punctata* (2 of 19), *Trionyx ferox* (5 of 31), *T. gangeticus* (1 of 7), and *T. hurum* (1 of 5). More frequent neural isolation occurs only in the two species of *Cyclanorbis*. Siebenrock (1902) discussed the marked variability of the neural series in these two species in his paper which established the existence of the two forms on osteological grounds. Both *Cyclanorbis* species can have long continuous rows of neurals or many isolated neurals. Although *C. senegalensis* tends to have more isolated neurals than *C. elegans*, the most reliable diagnostic features of these two species are found in the plastron. *C. senegalensis* is unique among living trionychids in possessing gular callosities. *C. elegans* is unique among cyclanorbines in having callosities of the fused hypo-hyoplastra that are flat or concave along their anterior edge.

The number of neurals appearing on the surface of the carapace in trionychids varies from 3 to 10. The occurrence of a tenth neural is very rare (3 of 242 specimens, two *Trionyx*...
subplanus and one T. cartilagineus) and seems to be anomalous. Thus, nine neurals make up the most complete series, and the possession of nine neurals is considered to be the fundamental condition for trionychids. This is not supported by evidence from the outgroups. All other members of this superfam-

Looking outside of the Trionychoidea, one finds nine neurals commonly in the Chelydridae, where they are packed closely together posteriorly. In the Cheloniidae, Chelonia my-
dos and Eretmochelys imbricata frequently have two neurals between the first pair of pleurals, as is proposed to be primitive for trionychids (see, for example, fig. 8 in De-

Variation in the number of neurals among living trionychids is given in table 5. The number of neurals (character 14, tables 1, 3) is treated as five character states, with nine neurals considered most primitive and seven or fewer neurals most derived.

Nearly all neurals of trionychids are six-
sided (see figs. 4, 5). Anterior and posterior ends of each neural contact adjacent neurals, the four lateral sides contact four adjacent pleurals, but the anterior and posterior pairs of pleural contacts are of unequal length, one usually being significantly longer than the other. In the anterior part of the neural series the shorter pleural contacts face posteriorly, but in the posterior part of the series (in most species) the shorter contacts face anteriorly. Thus, there is usually a reversal in orientation of these anterioposteriorly asymmetrical elements in every neural series.

Reversal of orientation occurs in two ways. More commonly it occurs via a four-sided neural (=a “diaphragmatic” neural of Hum-

With the exception of the Trionychidae, the margin of all testudine carapaces is solid. This is due to the presence of peripheral bones that form a complete ring around the carapace. In nearly all turtles this ring is composed of 22 peripheral elements, a nuchal and a pygal. Only in the Trionychoidea is there reduction and complete loss of these elements. In all kinosternids and Carettochelys there is one fewer peripheral on each side (total of 20). Peripherals 2 through 10 in Carettochelys are not sutured to the pleurals, which is also true for the only trionychid which retains bones in the periphery, Liss-

The homologies of the bones in the per-

SHELL PERIPHERY

With the exception of the Trionychidae, the margin of all testudine carapaces is solid. This is due to the presence of peripheral bones that form a complete ring around the carapace. In nearly all turtles this ring is composed of 22 peripheral elements, a nuchal and a pygal. Only in the Trionychoidea is there reduction and complete loss of these elements. In all kinosternids and Carettochelys there is one fewer peripheral on each side (total of 20). Peripherals 2 through 10 in Carettochelys are not sutured to the pleurals, which is also true for the only trionychid which retains bones in the periphery, Liss-

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SHELL PERIPHERY

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TABLE 7

Number of Reversals of Orientation in the Neural Series of Recent Trionychids

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* Number of reversals is given as a frequency. *Trionyx formosus, T. nigricans, and T. swinhoei* are excluded due to insufficient sample sizes; in *Cyclanorbis senegalensis* the neural series is too fragmented to allow the detection of reversals.

TABLE 8

Modal Character States for Shell Characters of the Recent Trionychidae Used in Analysis of Interfamilial Relationships

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* For descriptions of characters and character states see table 1.

* Except in kinetic forms.

gerl (1969), and others have considered these bones to be neomorphic structures. Walther (1922), Webb (1982), and Meylan (1985) have treated the peripherals of *Lissemys* as homologs of the peripherals of other turtles. Although these elements are found in the carapace only posterior to the bridge and they lack one-to-one correspondence with the pleurals, there is other evidence which suggests that they are degenerated peripherals and not neomorphs. In cross section the peripheral ossifications of *Lissemys* are like those of other turtles in that they consist of two laminar layers of bone which converge distally (fig. 7). Between these two layers is cancellous bone. *Lissemys* peripherals differ from those of other turtles principally in the absence of the proximal portion. Unless some developmental constraint that results in the formation of V-shaped elements in the periphery of all turtle shells can be identified, it may be best to consider these details of morphology as evidence of homology.

Peripherals are found in the carapace of *Lissemys* only posterior to the bridge and are usually about 18 in number (Deraniyagala, 1939). Peripherals are absent in all other trionychids. The reduction and loss of bones in the periphery is clearly derived (character 5, tables 1, 3, 8).

Although the rib heads of each pleural bone normally reach the centrum of the corresponding thoracic vertebra, the contact is not always a strong one. Only in trionychids and *Carettochelys* among the Cryptodira have I found strong, interlocking sutures (character 29, tables 1, 8). Richmond (1964) has suggested that the peripheral bones of most turtles form a locking ring between the arched carapace and the plastron, which acts as a tension member. This keeps the shell from expanding laterally when a dorsoventral force is applied. It is possible that these strengthened contacts between the rib-heads and vertebral centra may be an alternative means of countering such forces. Thus the carapace of *Carettochelys* may be "preadapted" for the loss of peripherals.

Both *Lissemys punctata* and *Cyclanorbis senegalensis* possess a prenuchal that is an isolated element that lies above the neck, just anterior to the nuchal (character 6, tables 1, 3). The prenuchal is a neomorph not found in any other cryptodire, and its appearance is a derived condition.
POSTERIOR END OF CARAPACE

In nearly all turtles, the eighth and last pair of pleurals forms as significant a portion of the carapace as those which precede it. Although the eighth pleurals of trionychids develop allometrically, being relatively larger in adult turtles than in juveniles, it is still possible to detect a difference in their size among species (compare figs. 4 and 5). In some forms they are large, in others somewhat reduced, and in yet others they are absent. The presence of large eighth pleurals provides a complete complement of pleural bones. The reduction of this complete complement is considered to be derived. Large eighth pleurals are present in all cyclanorbines as well as all Old World trionychines, except Trionyx euphraticus. There is a trend toward the loss of the eighth pleurals in New World forms (character 8, tables 1, 3).

The ilia of cyclanorbines, except Cyclanorbis elegans, articulate with the eighth pleurals, as they do in other cryptodires. In all trionychines and in C. elegans the ilia articulate with the tough connective tissue just posterior to the end of the shell. The presence of distinct areas of contact (either depressions or tubercles) for the ilia on the eighth pleurals (fig. 6B) is considered primitive, their absence derived (character 21, table 3).

PLastron

The plastron of most cryptodires includes nine elements (one pair each of epi-, hyo-, hypo-, and xiphiplastra and a single entoplastron). These nine elements are usually well sutured to one another and form a solid bony structure. The same nine elements are present in all trionychids (Bramble and Carr, MS), but they are relatively incomplete; they are often not sutured to one another and do not result in a single solid structure. Where plastral sutures are present in trionychids they occur
between the superficial dermal callosities with minor contributions from underlying elements. The presence of sutures, and thus of the callosities that allow them to occur, is interpreted as a primitive condition.

A suture is found between the hyo- and hypoplastra of all trionychids, and, in many, fusion occurs along this suture. The xiphiplastral callosities make contact at the midline in large Lissemys, Cycloderma, and Trionyx, but only in Lissemys punctata and Cycloderma aubryi does a sutured contact occur. This suture fuses in very old individuals of these two species. Sutures are absent between epi- and entoplastron, entoplastron and hypoplastra, hypo- and xiphiplastra, and along the midline (except for the xiphiplastra of the two species noted above) in all Recent trionychids.

The number of plastral callosities in all
trionychids increases with age but is stable in large adults (character 9). Callosities are present on all nine plastral elements in certain species and this is proposed as the primitive condition (fig. 8A, B). The callosities covering the hyo- and hypoplastron on each side are here considered to be a single structure making seven the primitive number. Seven callosities are found in *Lissemys*, *Cycloderma*, and some *Trionyx*. Derived conditions include both an increase and a decrease in the number of callosities (character 9, tables 1, 3). Only *Cyclanorbis senegalensis* has increased the number of callosities by the addition of a gular pair. The cyclanorbine *Cyclanorbis elegans* parallels the trend in the Trionychinae in having marked reduction in the number of callosities to two.

Although the fusion of two plastral elements is certainly derived, it can occur only when the primitive condition, a suture between two elements, is present. Thus the xiphiplastral suture in *Lissemys punctata* and *Cycloderma aubryi* suggests that they are primitive. However, xiphiplastral fusion is unique to these forms among trionychids and is considered a shared derived state (character 12, table 3).

Hyo-hypoplastral sutures occur at some stage in the ontogeny of all extant trionychids. Recent cyclanorbines share the common character state of hyo-hypoplastral fusion at a very small size (as small as 62 mm disc length). Fusion of the hypoplastra to the entoplastron occurs in all adult *Trionyx ferox* (fig. 8D) and in adults of some populations of *T. triunguis*. Hyo-hypoplastral fusion is considered to be derived and to occur independently in cyclanorbines and trionychines (characters 10 and 11, tables 1, 3).

The xiphi-hypoplastral union in trionychids is of two types. In all trionychines the two anterior xiphiplastral processes lie on either side of the most lateral of the three posterior processes of the hypoplastron (fig. 8C, D). In cyclanorbines the two anterior processes of the xiphiplastron lie on either side of the middle of the three posterior processes of the hypoplastron (fig. 8A, B). The trionychine condition occurs in chelonids, *Carettochelys*, and among kinosternids (*Kino sternon*, *Sternotherus*, and *Staurotypus*), suggesting that it is the primitive condition. Thus the presence of the hypoplastron lateral to the xiphiplastron at their junction is considered to be a derived condition unique to cyclanorbine trionychids (character 13, table 3).

Relative to the epiplastra of other Testudines those of trionychids are quite reduced in basic structure. The deep element, which may or may not be covered by a callosity, is I- or J-shaped. The J-shaped elements have a long ramus that is oblique to the midline and has a long contact with the entoplastron (fig. 8C, D). They also have an anterior projection of variable length that roughly parallels the midline. I-shaped elements consist of only the anterior portion and have minimal contact to the entoplastron (fig. 8B). J-shaped epiplastra are found in all trionychids except *Lissemys punctata*, *Cycloderma aubryi*, and *Cycloderma frenatum*, which have the alternate I-shape.

Long medial contact between the epiplastra and the entoplastron occurs in all non-trionychid turtles in which these elements are present. The posterior contact of the J-shaped epiplastra to the entoplastron maintains this contact and thus the J-shape is considered primitive, the I-shape derived (character 19, table 3).

The anterior extension of J-shaped epiplastra varies in length among the species in which it is found (compare fig. 8C and 8D). The extension beyond the entoplastron varies from 0.16 to 0.48 times the width of the hypoplastron of the right side (table 9). It is difficult to be certain which length of the extension is primitive for trionychids but it seems clear that the marked extension of *Trionyx cartilagineus*, *T. subplanus*, *T. sinensis*, and *T. steindachneri* is derived. As suggested by De Broin (1977), the species of the Indian subcontinent have epiplastra of intermediate length relative to the most elongate forms and other trionychids. Variation in this feature is treated as three states of character 20 with the longest extension considered to be most derived (character 20, table 3).

The boomerang shape of the entoplastron of trionychids is unique among turtles (character 22, table 8). Zangerl (1939) has implied that a T-shaped entoplastron is primitive for reptiles. The entoplastron in trionychids apparently arises from a proliferation and bend-
TABLE 9

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<td>0.014</td>
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<tr>
<td>tringuis</td>
<td>3</td>
<td>0.228</td>
<td>0.023</td>
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</table>

* Sample size, average, and one standard deviation are given for each species. Species with I-shaped epiplastra and T. nigricans are not included.

...
concern about the validity of characters of the size and shape of the jaws (Boulenger, 1889; Ylikeri, 1958; Barghusen and Parsons, 1966; Eisele, 1976; De Broin, 1977). But only Dalrymple's (1977) account of variation in the skull of *Trionyx ferox* treats the correlation of skull size and shape to environmental factors in a detailed and systematic fashion. Dalrymple has found that the most variable features of size and shape of the skull of *T. ferox* are those which relate to feeding. Those structures which provide sites of origin or passage for jaw musculature increase allometrically with age, and the amount of relative increase is highly variable. Furthermore, the development of features related to feeding can occur independently of one another. This high degree of variability in characters of the feeding apparatus indicates that they are not useful systematic features, as had been suspected.

In this study quantitative characters of the jaws and associated structures (palatal groove, supraoccipital spine) are avoided. Treatment of the skull concentrates on contacts between elements and on contacts between elements and features of external morphology. Because complete interspecific comparison is the goal of this study, data from sectioned skulls (8 of 22 trionychid species available) will not be treated. This is the first study of trionychid systematics for which at least one skull of every currently recognized Recent species was available.

The skull characters and character states which are treated in this section are summarized in table 10. The details of distribution of the states of characters important for resolving relationships within the Trionychidae are given in table 11. The states for characters important for resolving interfamilial relationships are given in table 12. Character states which are autapomorphic for a living trionychid species are listed in table 13. Discussion of these characters is arranged by region of the skull beginning anteriorly and proceeding posteriorly, with the dorsal surface treated first.

**Nasal Region**

The premaxillae of cryptodires are usually paired elements that make up the ventral edge of the apertura narium externum (fig. 9B). Among trionychoids this is true only for dermatoemydids and kinosternids. In *Carettochelys*, as well as all trionychids, these normally paired elements are fused to one another (character 44, tables 10, 12; figs. 9A, C, D, 10A, B). In trionychids this fused premaxillary differs further from those of the outgroups in being excluded from the apertura narium externum by the maxillae which meet dorsal to it (character 45, table 12; figs. 9A, C, 10A, B).

In three trionychids the premaxillary is either often absent (*Chitra indica*, 4 of 10), or nearly always absent (*Cycloderma frenatum*, 4 of 5; *Pelochelys bibroni*, 6 of 7) (character 65, table 11). The absence of this element is clearly derived.

Because nasals are absent in all trionychids, as they are in all living cryptodires (Gaffney, 1979b), the prefrontals are the anteriormost paired elements on the dorsal surface of the skull. Thus, the prefrontals form the dorsal border of the apertura narium externum. Laterally these elements contact the maxillae and border the anterior portion of each orbit between the maxilla and frontal. In most cryptodires the descending processes of the prefrontals contact the vomer and palatines. There is significant variation among trionychids in these contacts. There is also useful variation in the degree of emargination of the prefrontals at the dorsal edge of the apertura narium externum and in the degree of separation of the maxillae and frontals along the anterior margin of the orbit.

Through reduction of the prefrontals, vomer, and palatines, contact between the prefrontals and palatal elements in trionychids is greatly reduced, or lost. The prefrontal-palatine contact found in most cryptodires is lost in all trionychids (Gaffney, 1979b) and this loss can be considered a shared derived character for the family (character 38, table 12). Contact between the vomer and prefrontals is the common condition among trionychids, as it is for all testudines (fig. 10A). It is absent only in *Cycloderma aubryi*, *Cycloderma frenatum*, *Cyclanorbis senegalensis* and *Chitra indica* (fig. 10B), and is clearly a derived condition (character 36, table 11).

With the exception of two very primitive forms, *Proganochelys* and *Kallokibotion*, testudines have an unpaired apertura narium externum with a nearly straight to somewhat
<table>
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<tr>
<th>Characters</th>
<th>Character states</th>
<th>52. processus pterygoideus externus projects from pterygoid</th>
<th>53. size of foramen palatinum posterius</th>
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<td>2. occasionally</td>
<td>2. small</td>
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<td>33. quadratojugal contacts postorbital</td>
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<td>3. no</td>
<td>3. small and divided</td>
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<td>34. jugal contacts parietal on skull surface</td>
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<td>4. many small openings</td>
<td>4. many small openings</td>
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<td>35. jugal contacts parietal within fossa temporalis</td>
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<td>36. vomer contacts prefrontal</td>
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<td>37. incisura columella auris closed</td>
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<td>38. palatines contact prefrontals lateral to vomer</td>
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<td>39. cheek emargination extends above lower edge of orbit</td>
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<td>42. dorsal edge of apertura narium externum medially emarginate</td>
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<td>43. palatine forms a significant part of the lateral wall of the braincase</td>
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<td>44. premaxillae fused into single element</td>
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<td>45. premaxillae enter apertura narium externum</td>
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<td>47. foramen intermaxillaris</td>
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<td>48. vomer divides maxillae</td>
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<td>49. vomer reaches intermaxillary foramen</td>
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<td>50. vomer contacts pterygoid</td>
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<tr>
<td>51. vomer contacts basisphenoid</td>
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<td>1. yes</td>
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<td>2. no</td>
<td>2. palatine only</td>
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<td>54. foramen palatinum posterius forms in</td>
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<td>3. no</td>
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<td>55. basis tuberculi basalis present</td>
<td>4. yes</td>
<td>4. yes</td>
<td>4. yes</td>
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<td>56. foramen posterus canalis carotic interni completely within pterygoid</td>
<td>1. no</td>
<td>1. no</td>
<td>1. no</td>
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<td>57. canalis carotic interni straight and wide</td>
<td>2. yes</td>
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<td>2. yes</td>
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<td>58. foramen jugulare posteriorius excluded from fenestra postotica by pterygoid arching to contact opisthotic</td>
<td>1. no</td>
<td>1. no</td>
<td>1. no</td>
</tr>
<tr>
<td>59. foramen jugulare posteriorius excluded from fenestra postotica by descending process of opisthotic which reaches pterygoid</td>
<td>2. yes</td>
<td>2. yes</td>
<td>2. yes</td>
</tr>
<tr>
<td>60. foramen posterus canalis carotic interni relative to lateral crest of basioccipital tubercle</td>
<td>1. above</td>
<td>1. above</td>
<td>1. above</td>
</tr>
<tr>
<td>61. groove for some portion of stapedial artery visible on prootic or descending process of paretal</td>
<td>2. in it</td>
<td>2. in it</td>
<td>2. in it</td>
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<tr>
<td>62. maxilla contacts frontal in front of orbit</td>
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<td>63. exoccipital contacts pterygoid</td>
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<td>64. basisphenoid shape</td>
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<td>65. premaxilla absent</td>
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<td>66. vomer lost</td>
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<td>67. jugal contacts orbit</td>
<td>2. yes</td>
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TABLE 10—(Continued)

<table>
<thead>
<tr>
<th>Characters</th>
<th>Character states</th>
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</table>
| 68. epipterygoid, if present, contacts the palatine | 1. yes  
| | 2. in ca. 50%  
| | 3. no  
| 69. contact between pterygoid and foramen nervi trigemini occurs when epipterygoid is present | 1. yes  
| | 2. no  
| 70. when epipterygoid is present pterygoid contacts foramen nervi trigemini | 0. between epipterygoid and quadrate or not at all  
| | 1. between prootic and epipterygoid or not at all  
| | 2. between epipterygoid and parietal or not at all  
| 71. epipterygoid contacts prootic anterior to foramen nervi trigemini | 1. no  
| | 2. in ca. 50%  
| | 3. yes  
| 72. epipterygoid contacts prootic posterior to foramen nervi trigemini | 1. no  
| | 2. yes  
| 73. epipterygoid fuses to pterygoid | 1. in subadults  
| | 2. in adults only  
| | 3. never  
| 74. average ratio of intermaxillary foramen length to length primary palate | 0. 0.07  
| | 1. about 0.20 to 0.40  
| | 2. about 0.60  
| | 3. 0. about 2 times orbit diameter  
| | 1. about equal to orbit to 1/3 of orbit  
| | 2. less than 1/4 of orbit  
| 75. postorbital bar relative to orbit | 0. about 2 times orbit diameter  
| | 1. about equal to orbit to 1/3 of orbit  
| | 2. less than 1/4 of orbit  
| 76. quadratojugal participates in processus trochlearis oticum | 1. no  
| | 2. yes  
| 77. quadrate make-up of the processus trochlearis oticum | 1. greater than 50%  
| | 2. 33 to 50%  
| | 3. less than 33%  
| 78. proportion of processus trochlearis oticum made up by parietal | 1. 15.6% or less  
| | 2. 22.1% or more  

anteriorly convex dorsal margin that is usually formed by the prefrontals (fig. 9B, D). This is true for the outgroups and for some living species of trionybrids. The remaining trionybrids show some degree of emargination of the prefrontals and thus alteration of this primitive shape of the external narial opening. With one exception emargination occurs laterally and is either shallow (fig. 9A) or quite deep (fig. 9B) (character 41, table 11). Only in Cyclanorbis elegans does emargination occur medially (character 42, table 13). The condition in C. elegans is considered to occur independently from that in other emarginate forms. Weak lateral emargination is considered to be intermediate between the strongly emarginate and nonemarginate conditions.

It is the prefrontal that normally separates the maxilla from the frontal at the anterior edge of the orbit in turtles. In a single trionychid, Trionyx subplanus, the maxillae contact the frontals lateral to the prefrontals in about one-half of the specimens examined. In the others, these elements are quite close and their proximity can be considered a unique feature of this species (character 62, table 13).

**Orbital Region**

A frequently used character in trionychid systematics is the relationship between the width of the postorbital bar and orbit diameter (character 75). The postorbital bar varies in width among the species of this family from two times wider than the orbit to one-sixth of orbit width (fig. 11). Variation in the width of the postorbital bar relative to the width of the orbit is not continuous but constitutes four separate sets of species. The outgroups vary in width of postorbital bar between state two (equal to or wider than orbit) and state three (one-half to one-third width of orbit). Only Claudius, with a very narrow postorbital bar (state 4), and Platy sternon and the chelonoids, which lack temporal emargination (state 1), show the extreme conditions. In the current context it seems most appropriate to consider most divergent postorbital bar widths to be derived relative to the combined intermediate groups.

**Skull Emargination**

The advanced cryptodires (Chelomacryptodira of Gaffney, 1984), the Trionychoidea and Testudinoidea, have highly developed temporal emargination. But these two superfamilies differ greatly in the degree of cheek emargination that they exhibit.

As reviewed by Gaffney (1979b) there has always been a problem identifying landmarks
Table 11
Character States for Characters of the Trionychid Skull Useful in Assessing Intrafamilial Relationships

| Characters | Species | 32 | 34 | 36 | 48 | 49 | 53 | 54 | 58 | 60 | 64 | 65 | 68 | 69 | 70 | 71 | 72 | 73 | 74 | 75 | 76 | 78 |
|------------|---------|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|
| aubryi     | 1 3 2 2 2 2 4 2 2 1 3 1 1 1 2 2 | | | | | | | | | | | | | | | | | | | | | |
| bibroni    | 1 3 1 1 1 1 2 1 1 1 2 1 3 3 1 0 2 1 2 | 1 1 | 1 | 1 | 1 | 1 | | | | | | | | | | | | | | | | |
| cartilagineus | 1 1 1 2 2 2 1 1 1 2 2 1 2 1 2 1 0 2 1 3 1 2 1 1 | | | | | | | | | | | | | | | | | | | | | |
| elegans    | 1 3 1 1 2 2 3 2 2 1 3 1 1 3 2 | | | | | | | | | | | | | | | | | | | | | |
| euphraticus | 1 1 1 2 1 1 2 1 1 1 3 2 1 1 1 0 1 1 3 2 1 2 | 2 | | | | | | | | | | | | | | | | | | | | |
| ferox      | 1 1 1 3 1 1 1 1 1 3 1 1 1 3 1 0 1 1 3 2 1 2 | 2 | | | | | | | | | | | | | | | | | | | | |
| formosus   | 2 3 1 2 2 2 2 1 1 1 3 3 1 1 1 1 1 1 3 1 1 1 1 | | | | | | | | | | | | | | | | | | | | | |
| frenatum   | 1 3 2 1 2 2 4 2 2 1 3 1 2 3 2 | | | | | | | | | | | | | | | | | | | | | |
| gangeticus | 1 1 1 2 2 2 1 1 1 3 3 1 1 1 | | | | | | | | | | | | | | | | | | | | | |
| harum      | 1 2 1 3 2 2 2 | | | | | | | | | | | | | | | | | | | | | |
| indica     | 1 3 2 1 1 1 2 1 1 1 2 1 2 3 1 0 3 1 3 0 1 | 1 | | | | | | | | | | | | | | | | | | | | |
| leithii    | 2 2 1 2 2 2 1 1 1 3 3 1 1 | | | | | | | | | | | | | | | | | | | | | |
| muticus    | 2 2 1 3 1 2 2 1 1 1 3 1 1 1 2 | | | | | | | | | | | | | | | | | | | | | |
| nigricans | 2 1 1 2 2 2 2 1 1 1 2 3 1 3 1 1 1 1 3 1 1 1 | | | | | | | | | | | | | | | | | | | | | |
| punctata   | 1 2 1 3 1 2 2 2 1 3 1 2 1 1 1 1 | | | | | | | | | | | | | | | | | | | | | |
| senegalensis | 1 3 2 2 1 1 3 2 2 2 | | | | | | | | | | | | | | | | | | | | | |
| sinensis  | 2 2 1 3 2 2 2 1 2 3 3 1 1 1 1 2 1 1 1 3 1 1 2 1 1 1 1 | | | | | | | | | | | | | | | | | | | | | |
| spiniferus | 1 1 1 3 1 1 2 1 1 1 3 2 1 | | | | | | | | | | | | | | | | | | | | | |
| steindacheri | 1 3 1 3 2 2 1 1 1 3 2 1 | | | | | | | | | | | | | | | | | | | | | |
| subplanus | 1 2 1 3 2 2 2 1 1 2 3 2 1 | | | | | | | | | | | | | | | | | | | | | |
| swinhoei | 2 1 1 2 1 1 2 2 2 1 3 1 | | | | | | | | | | | | | | | | | | | | | |
| triunguis | 1 1 1 3 2 2 2 1 1 1 3 1 1 1 3 1 1 1 0 1 1 3 2 1 2 2 | | | | | | | | | | | | | | | | | | | | | |

* Numbers refer to character states outlined in table 10.

Table 12
States of Skull Characters Important in Interfamilial Analyses

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<tr>
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</table>

* Numbers represent the character states listed in table 10.
Fig. 9. Frontal views of the skull of four cryptodiran turtles showing fusion of the premaxillae (stippled) in trionychids (A, B) and carettochelyids (D), exclusion of the premaxillae from the aperture narium externum in trionychids (A, B), and slight (A) to extensive (B) emargination of the anterior border of the prefrontals. A. *Trionyx cartilagineus* (RH i29); B. *T. ferox* (AMNH 129737); C. *Chelonia mydas* (UF 55880); D. *Carettochelys insculpta* (UF 43888).

visible over a significant distance. With this degree of temporal emargination the postorbital bone, which makes up a significant portion of the postorbital bar, is usually exposed. This is true for all outgroup trionychoids and testudinoids examined. The postorbital in trionychids is one of several skull elements which has undergone extreme reduction. This reduction is so extreme that contact between the jugal and parietal occurs below the skull surface in all trionychids (character 35, table 12) and these two elements make up much of the postorbital bar. In some trionychids jugal-parietal contact is so strong that it is present on the skull surface and the postorbital is isolated from the temporal emargination (fig. 11A, B). Isolation of the postorbital from the temporal emargination might seem quite primitive and it certainly is if isolation is via parietal-squamosal or parietal-squamosal-quadratojugal contact. But isolation via jugal-parietal contact is a derived feature found only among trionychids. Jugal-parietal contact on the skull surface can vary within a single trionychid species. This variable condition is considered to be intermediate between the primitive absence of jugal-parietal contact on the skull surface and its presence which is certainly derived (character 34, table 11).

Lateral to the temporal emargination in trionychids is a very narrow bar formed by the jugal and quadratojugal. The trionychids parallel the condition seen in some emydids
TABLE 13
Autapomorphic Skull Features of Trionychid Turtles

<table>
<thead>
<tr>
<th>Character</th>
<th>Species</th>
<th>Autapomorphic state</th>
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<tr>
<td>42</td>
<td>Cyclanorbis elegans</td>
<td>apertura narium externum medially emarginate</td>
</tr>
<tr>
<td>46</td>
<td>Trionyx euphraticus</td>
<td>basisphenoid fails to contact palatines</td>
</tr>
<tr>
<td>51</td>
<td>Pelochelys bibroni</td>
<td>vomer contacts basisphenoid</td>
</tr>
<tr>
<td>62</td>
<td>Trionyx subplanus</td>
<td>maxillae contact frontals in orbit</td>
</tr>
<tr>
<td>63</td>
<td>Trionyx triunguis</td>
<td>pterygoid isolated from exoccipital by basioccipital</td>
</tr>
<tr>
<td>66</td>
<td>Cycloderma frenatum</td>
<td>jugal excluded from orbit</td>
</tr>
<tr>
<td>67</td>
<td>Cycloderma aubryi</td>
<td>foramen intermaxillaris quite reduced</td>
</tr>
<tr>
<td>74</td>
<td>Chitra indica</td>
<td>postorbital bar one-ninth of orbit diameter</td>
</tr>
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</table>

Fig. 10. Anterior view of the skulls of two trionychid turtles. A. Trionyx triunguis (BMNH 1947.3.6.12); B. Cyclanorbis senegalensis (BMNH 65.5.9.20); both from Loveridge and Williams (1957).

of extreme quadratojugal reduction. But unlike the case in emydids this element is never lost. In all trionychids the quadratojugal contacts only the jugal and not the maxilla or postorbital anteriorly. Posteriorly it sutures to the quadrate and squamosal. In other living trionychoids the contact of the quadratojugal to the postorbital is maintained and the quadratojugal maxillary contact is maintained except in some Dermatemys (UF 29168; fig. 172 in Gaffney, 1979b). Reduced contact of the quadratojugal is considered derived within the Trionychoidea (characters 31 and 33, table 12).

Because of the reduced size of the quadratojugal, the jugal and squamosal lie quite close to one another in all trionychids. In six species they are occasionally in contact. This is considered to be a derived condition (character 32, table 11).

Strong cheek emargination, which accompanies temporal emargination in testudinoids, is not found among living trionychoids. Although cheek emargination is visible in Dermatemys, Carettochelys, and kinosternids, it does not extend above a line extending horizontally from the lower edge of the orbit (character 39, table 12). In testudinoids, on the contrary, cheek emargination is quite well developed and extends well dorsal to such a line (except in Malayemys). In all testudinoids and trionychoids except for the Trionychidae, cheek emargination is limited anteriorly by the maxillary. In the Trionychidae, cheek emargination occurs within the jugal when it is present (character 40, table 12). Because of flexure of the snout in trionychids, ventral emargination of the jugal does reach above the lower rim of the orbit in a few cases. But emargination occurs only within the jugal and is the site of origin of the M. zygomatico-mandibularis (Dalrymple, 1977), a muscle which is unique to trionychids. Therefore, it is likely that cheek emargination in trionychids is not homologous to that of other turtles and that restriction of true cheek emargination ventral to the lower.
Fig. 11. Dorsal view of the skulls of three trionychid turtles. **Top**, *Trionyx triunguis* (BMNH 1947.3.6.12), from Loveridge and Williams (1957); **middle**, *Chitra indica* (from Gray, 1855, presumably BMNH specimen, sutures added from MCZ 29487); **bottom**, *Cyclanorbis senegalensis* (BMNH 65.5.9.20), from Loveridge and Williams, 1957.)
TABLE 14
Average Contribution of Quadratojugal, Quadrate, Prootic, and Parietal to the Processus Trochlearis Oticum of Recent Trionychid Turtles

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<th>Species</th>
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<th>Prootic</th>
<th>Parietal</th>
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</thead>
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<tr>
<td>aubryi</td>
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<td>0.000</td>
<td>0.227</td>
<td>0.607</td>
<td>0.166</td>
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<tr>
<td>bibroni</td>
<td>7</td>
<td>0.000</td>
<td>0.207</td>
<td>0.602</td>
<td>0.117</td>
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<tr>
<td>cartilagineus</td>
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<td>0.007</td>
<td>0.239</td>
<td>0.655</td>
<td>0.139</td>
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<tr>
<td>elegans</td>
<td>5</td>
<td>0.011</td>
<td>0.236</td>
<td>0.565</td>
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<td>euphraticus</td>
<td>9</td>
<td>0.020</td>
<td>0.166</td>
<td>0.557</td>
<td>0.266</td>
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<td>ferox</td>
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<td>formosus</td>
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<td>0.000</td>
<td>0.294</td>
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<td>frenatum</td>
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<td>0.026</td>
<td>0.130</td>
<td>0.734</td>
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<td>gangeticus</td>
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<td>0.007</td>
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<td>0.720</td>
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<td>hanum</td>
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<td>0.213</td>
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<td>indica</td>
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<td>0.312</td>
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<td>leutilii</td>
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<td>0.004</td>
<td>0.189</td>
<td>0.584</td>
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</table>

rim of the orbit can be considered a derived feature of the Trionyochoidea (character 39, table 12).

STAPEDIAL FORAMEN

The most significant difference between testudinoids and trionychoid turtles is in the pattern of blood flow to the head (McDowell, 1961; Albrecht, 1967; Gaffney, 1975, 1979b). This is reflected in variation of the size of the stapedial foramen and in the morphology of the prootic and parietal adjacent to this foramen. In testudinoids the majority of anterior blood flow is via the stapedial artery. Therefore the foramen stapediopemorale is large and there is often a groove in the prootic and parietal for the large stapedial artery. In trionychoids, the stapedial artery is reduced because most of the anterior blood flow is via the internal carotid artery. In this superfamily the foramen stapediopemorale tends to be reduced or absent and rarely is there evidence of a groove for the stapedial artery on the prootic or parietal (character 61, table 12). These features are important at the family level, there is little variation within the Trionychidae.

PROCESSUS TROCHLEARIS OTICUM AND QUADRATE

The processus trochlearis oticum is a distinctive feature of the Cryptodira. It is over this structure that the majority of the jaw adductor musculature lies. This is in contrast to the condition in Pleurodira in which the lower jaw adductors slide over a process of the pterygoid. In most cryptodires the majority of the processus is formed by the quadrate.

In trionychids the processus trochlearis oticum can be quite large and always involves the quadrate, prootic, and parietal (table 14). In 13 species the quadratojugal is included in at least some individuals (fig. 11 top). Within the Trionychidae, three useful patterns of variation are noted: the inclusion of the quadratojugal in the processus trochlearis oticum, reduction in the contribution made by the quadrate, and increase in the contribution made by the parietal. The first occurs when the quadratojugal sends a medial process across the anterior edge of the quadrate (fig. 11 top). It results in reduction of the quadrate contribution and is absent from all outgroups. It is thus considered to be derived within the Trionychidae (character 76, table 11). In trionychids, unlike essentially all other cryptodires, the quadrate makes up less than one-third of this structure (character 77, table 12).

There is additional variation among trionychids in the amount of parietal contribution. In the majority the parietal contribution is small, always less than one-sixth of the total (table 14). In the North American forms, and also Cyclanorbis elegans, Trionyx euphraticus, T. nigricans, T. swinhoei, and T. triunguis the parietal contribution is slightly larger, about one-fourth or more of the processus trochlearis oticum (character 78, table 11). The contribution of the parietal to this structure in other cryptodires is quite limited or absent. Thus the large contribution in trionychids is clearly derived.

In very few chelonians does the quadrate
Fig. 12. Right lateral views of the skull of three cassichelydians with portions removed to expose trigeminal region. A, Solnhofa parsoni (Teyler Museum 4023); B, Emyndura sp. (AMNH 72418); C, Chelydra serpentina (AMNH 9249).
Fig. 13. The trigeminal region of eight trionychoid turtles showing contacts of the skull elements around the foramen nervi trigemini and participation by the palatine in the lateral wall of the braincase. The foramen interorbitale is crosshatched; the foramen nervi trigemini is stippled. Abbreviations: e, epipterygoid; pal, palatine; pa, parietal; pr, prootic; pt, pterygoid; qu, quadrate. A. Dermatemys mawii (BMNH 1911.1.28.1); B. Staurotypus salvinii (BMNH 1879.1.7.5); C. Carettochelys insculpta (BMNH 1903.4.10.1); D. Lissemys punctata (UF 56017); E. Cyclanorbis elegans (BMNH 1954.1.14.3); F. Trionyx hurum (BMNH 86.8.16.2); G. Trionyx triunguis (BMNH 62.3.20.8); H. Chitra indica (IRSB 3295).
completely surround the columella (Gaffney, 1979b). Among cryptodires this occurs in the Trionychidae, Carettochelys, Chelydridae, and most Testudinidae (tables 10, 12).

TRIGEMINAL REGION

The trigeminal foramen lies lateral to the braincase and ventral to the processus trochlearis oticum of cryptodires (figs. 12, 13). In trionychids it is a large opening providing an exit for the maxillary and mandibular branches of the trigeminal nerve as well as the mandibular artery (Gaffney, 1979b). In trionychids the parietal, prootic, quadrate, pterygoid, and epipterygoid may contact this foramen but there is significant inter- and intraspecific variation in the degree and form of contact of each element (fig. 13).

An epipterygoid is present in all trionychid species but tends to fuse to the pterygoid in larger individuals (table 15). Fusion occurs less frequently (perhaps later in life) in trionychids than in cyclanorbines. Variation in the length of retention of a distinct epipterygoid is treated via three states of character 73 (tables 10, 11). This element usually fuses to the pterygoid in older adults of most cryptodires. Long-term retention of the epipterygoid is therefore considered to be a derived feature.

Because the epipterygoid is an important landmark in describing variation in the morphology of the trigeminal region of trionychids, descriptions of this region are based on individuals in which this element is not yet fused to the pterygoid. The contacts described are those visible on the outside of the skull (as seen in fig. 13); in some cases internal contacts will differ. Complication of these descriptions arises because the epipterygoid is a superficial element of variable shape and size that can cover certain contacts in some individuals of a given species but not in others. This results in the ungainly appearance of the three states of character 73 (tables 10, 11). This element usually fuses to the pterygoid in older adults of most cryptodires. Long-term retention of the epipterygoid is therefore considered to be a derived feature.

Table 15

<table>
<thead>
<tr>
<th>Species</th>
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<th>B</th>
<th>C</th>
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</table>

*Condylar length (in mm) of the largest skull with a free epipterygoid (A), the smallest skull with a fused epipterygoid (B), and largest skull measured (C) are given for each species.*

between the prootic and epipterygoid (state 1) (fig. 13B, D, F), ventrally between the pterygoid and quadrate (state 0), anteriorly between the parietal and epipterygoid (state 2), or in no individuals at all (character 69, state 2) (fig. 13E, G). See table 11 for distribution of these character states.

Contact of the pterygoid to the foramen nervi trigemini between the prootic and epipterygoid (state 1, character 70) occurs in Trionyx formosus, T. gangeticus, T. hurum, T. nigricans, and Lissemys punctata and results in the isolation of the quadrate from the foramen nervi trigemini (fig. 13D, F). In both Cyclanorbis species and both Cycloderma species the quadrate is also isolated from the foramen nervi trigemini. But in this case it is the epipterygoid that meets the prootic posteriorly and thus intervenes (character 71, state 2; fig. 13E). When the epipterygoid fuses to the pterygoid, the two groups mentioned above (those with state 1 of character 70 and
those with state 2 of character 71) look identical.

Significant variation in this region among the outgroups makes assigning polarities to characters of contact of the epitypogoyd to the foramen nervi trigemini difficult. Identification of polarity for other contacts in the trigeminal region seems clear. In no other trionychoid does the epitypogoyd contact the prootic posteriorly (fig. 13A, B, D) as it does in Cyclanorbis and Cycloderma (character 71, table 11; fig. 13E) or anteriorly as it does in some or all members of certain trionychine species (character 71, table 11; fig. 13H). Similarly, all trionychoid outgroups have contact between the epitypogoyd and palatine (fig. 13A-C) and the absence of this contact in some or all members of a species is considered derived (character 68, tables 10, 11).

An important feature of the Trionychoidea (sensu Gaffney, 1979b) is participation of the palatine in the formation of the lateral wall of the braincase. This occurs in all trionychoids examined and can be seen just anterior to the foramen nervi trigemini (fig. 13). In trionychoids the pterygoid is excluded from the interorbital fenestra by the expanded palatines. In testudinoids and in other turtles the pterygoid either reaches the interorbital fenestra or is immediately adjacent to it (character 42, table 12) (fig. 12).

### Occipital Region

There are numerous systematically useful characters visible on the skull in posterior view. One of these is a reflection of the importance of the internal carotid artery (Albrecht, 1967; McDowell, 1961; Gaffney, 1975, 1979b). The large diameter of the canalis caroticus interni and the straight path that it follows in trionychoids can be observed even in articulated skulls. A stiff wire, slightly narrower than the canal, will pass into the foramen posterius canalis caroticus interni and out of the foramen anterius canalis caroticus interni with ease (character 57, table 12). In large trionychids the latter opening is quite ventrally located and is reminiscent of the condition in the “Paracryptodira” (fig. 15C). However, in all other trionychoids and other Eucryptodira it is posteriorly located. Thus the presence of these foramina on the ventral surface of the skull is considered derived.

Variation in the location of the foramen posterius canalis caroticus interni within the Trionychidae is best described in relation to a crest of bone which is a lateral extension of the tuberculum basioccipitale. In no member of this family is this foramen located above such a crest, but in Pelochelys bibroni, Chitra indica, Trionyx cartilagineus, and T. nigricans (only one specimen available) it is found within the crest (see fig. 15; foramen posterior canalis caroticus interni is visible in A and C but not in B). The latter condition is considered to be primitive relative to the ventral position found in all other species (character 60, table 11).

The foramen jugularis posterior is located lateral to the foramen magnum in turtles and is visible in posterior view. In most cryptodires it is surrounded by the exoccipital or exoccipital and opisthotic (fig. 14A–C). In some cheloniods, some trionychids, and some Claudius and Platysternon, this opening is continuous with the fenestra postotica (fig. 14D). Isolation of the foramen jugularis posterior from the fenestra postotica when present in the Trionychidae occurs in a unique manner: that is, by contact of the pterygoid to the opisthotic (fig. 14E, F). In all cyclanorbines the pterygoid arches dorsally to meet the opisthotic (fig. 14F). In the trionychines, infrequent isolation occurs via the descent of
Fig. 14. Posterior views of the skull of six eucryptodiran turtles. A. *Macroclemys temminckii* (AMNH 58251); B. *Chinemys reevesii* (AMNH 31117); C. *Sternotherus odoratus* (AMNH 69752); D. *Pelochelys hiberni* (AMNH 23541); E. *Pelodiscus sinensis* (UF H 2406); F. *Lissemys punctata* (NMNH 61094).
a narrow process of the opisthotic across an otherwise open fenestra postotica (fig. 14E). These two types of isolation of the foramen jugulare posterius appear to be independent evolutionary events (Loveridge and Williams, 1957) and are treated as such in the analysis of intrafamilial relationship (characters 58 and 59, table 11).

In nearly all trionychids, as in most other trionychoids and in chelydrids (including Platysternon) and chelonii, there is contact between the exoccipital and pterygoid. Only in Trionyx triunguis does the basioccipital intervene between these elements, separating them as it does in most testudinoids. In the current context this is a unique feature most useful for the recognition of T. triunguis (character 63, table 13). Separation of the pterygoid from the exoccipital may be a shared derived feature of the Testudinida.

The basis tuberculi basalis is a small tubercle on the dorsal surface of the basioccipital found within the braincase. When present this tubercle is visible (under correct lighting) through the foramen magnum. Gaffney (1979b) reported that it is variably developed in most turtles but that it is missing in Trionyx ferox. I find this structure to be absent in all trionychoids and testudinids examined, but clearly visible in chelonii, dermochelydrids, chelydrids, and emydids (but not Rhinoclemmys pulcherrima). This is therefore a useful character at the interfamilial level (character 55, table 12).

**Palate**

The most striking differences between the palates of trionychids and those of other cryptodires is the presence of a median foramen anterior to the apertura narium internum and the presence of unconstricted pterygoids (fig. 15). This midline opening is usually of large size and is called the foramen intermaxillaris. It varies in size in the Trionychidae (see below, character 74) but it always separates the vomer from the fused premaxillae. The same structure appears to be present in Carettochelys where it is continuous with the apertura narium internum. In Carettochelys the vomer and maxillae do not meet anterior to the apertura narium internum and the posterior limits of the foramen intermaxillaris remain undefined.

A structure that appears to be homologous to the foramen intermaxillaris is present in mature individuals of all three living staurotyine kinostemids and in Xenochelys formosus (Oligocene of South Dakota, Williams, 1952). The deep pit in the premaxillae, which accommodates the symphysial projection of the lower jaw in all kinostemids, opens dorsally in large individuals of both species of Staurotyphus, in Claudius, and in Xenochelys. This does not occur in large individuals of any other living turtles with strongly hooked lower jaws such as chelydrids (including Platysternon). In staurotypines, this opening accommodates the sharply hooked symphysis of the lower jaws as it does in Carettochelys. Trionychids always have the foramen intermaxillaris in spite of the fact that they have unhooked lower jaws (character 47, table 12).

Variation in the size of the foramen intermaxillaris among trionychids has been utilized by several authors (Loveridge and Williams, 1957; De Broin, 1977). Comparison of the length of the foramen intermaxillaris relative to the total skull length is not satisfactory; the distribution of this character for trionychids is quite continuous (fig. 2). It should be noted, however, that the members of a proposed monophyletic group (Meylan, 1985), the North American forms plus Trionyx swinhoei, T. euphraticus, and T. triunguis, have the highest values for the ratio of foramen intermaxillaris length to total skull length.

This character can be utilized if examined in terms of foramen size relative to the primary palate. Variation in the ratio of length of the foramen intermaxillaris to length of the primary palate among trionychids falls into five distinct groups (fig. 2, table 10). Identification of a character polarity for the states of this character is difficult. The foramen intermaxillaris in other trionychoids is highly specialized in one case (Carettochelys) and incompletely developed in the other (Staurotypine). It appears prudent to assume that the medium size classes together approximate the primitive state and that the most divergent conditions (states 0 and 2) are
Fig. 15. Ventral view of the skulls of three trionychid turtles. Top, *Trionyx triunguis* (BMNH 1947.3.6.12, modified from Loveridge and Williams, 1957); middle, *Chitra indica* (from Gray, 1855, presumably BMNH specimen, sutures added from MCZ 29487); bottom, *Cyplanorbis senegalensis* (BMNH 65.5.9.20, from Loveridge and Williams, 1957).
derived within the Trionychidae (character 74, tables 11, 13).

The vomer is one of several elements which is reduced in the Trionychidae. In most turtles it lies between the paired maxillae and palatines. Anteriorly it reaches the premaxillae and posteriorly it often contacts the paired pterygoids. When a foramen intermaxillaris is present, premaxillary contact is prevented. In some trionychids the vomer divides the maxillae completely and reaches the foramen intermaxillaris between them (fig. 15C). This most closely approximates the condition in the outgroups in which no foramen intermaxillaris is present and is therefore considered to be the primitive condition for the relationship of the vomer to the maxillae (character 48, table 11).

In other trionychids the maxillae meet on the midline of the palate ventral to the vomer. Depending on the degree of reduction of the vomer and the length of this intermaxillary suture, the vomer may still enter the foramen intermaxillaris by reaching it dorsally over the united maxillae. Reduction of the vomer to the extent that it does not reach anteriorly to the foramen intermaxillaris is interpreted as the derived state of character 49 (table 11).

Posteriorly, the vomer of most cryptodires reaches between the paired palatines as far as the pterygoids. This is true of Dermatemys and kinosternids, but not Carettochelys or any trionychids (fig. 15). The failure of the vomer to reach as far posterior as the pterygoids is considered a derived condition (character 50, table 12).

In most chelonians the vomer is the only unpaired midline element reaching the transverse pterygo­palatine suture. In Carettochelys and all trionychids (except T. euphraticus), only an enlarged basisphenoid does so (fig. 15). This unique contact of palatal elements has been recognized as evidence of unique common ancestry of these two taxa (Baur 1891b; Meylan, 1985). It is treated as such here (character 46, table 12). The absence of contact of palatines and basisphenoid in most specimens of T. euphraticus appears to be a unique reversal (character 46, table 13).

The vomer of turtles does not normally contact the basisphenoid, but with the anterior extension of the latter in trionychids comes a greater possibility that such contact might occur. Siebenrock (1897) reports vomer-basisphenoid contact on the dorsal surface of the palate in Pelochelys. In two of the seven Pelochelys skulls examined during this study (USNM 231523 and NMW 1857), contact between these elements is present on the palate. This condition is unique to Pelochelys among the Trionychidae (character 51, table 13). In Cycloderma frenatum the vomer is absent. This is a unique condition among trionychids (character 66, table 13).

At or near the palatine-­pterygoid suture in all chelonians is located a paired ventral opening in the palate, the foramen palatinum posterius. This opening is never large in trionychids (fig. 15). It may be entire, divided into two openings, or divided into numerous small openings not larger than the nutritive foramina of the palate. Small size of these openings may be a feature shared by all trionychoids as well as some testudinoids, but the variation in the division of this opening is useful within the Trionychidae, and in particular among the Cyclanorbinae (character 53, table 11). Division of the foramen palatinum posterius is considered derived.

The contacts of the foramen palatinum posterius also vary among the living species of the Trionychidae. In most trionychids, as in most chelonians, these foramina contact the palatine and the pterygoid and/or maxillary. In a limited number of trionychids this opening is restricted to the palatine, which is considered to be a derived condition (character 54, table 11).

The processus pterygoideus externus of cryptodires usually takes the form of a moderate to short posterior or posterolateral projection from the anterolateral edge of the pterygoid just anterior to some degree of medial constriction. It is found in nearly all cryptodires and varies considerably in degree of development. In trionychids there is no medial constriction of the pterygoids and no free projection of this process (fig. 15). In Carettochelys, the pterygoids are only slightly constricted and the processus pterygoideus externus projects very weakly or not at all. In other trionychoids these processes may be present (Kinosternon, Staurotypus, some Dermatemys, some Claudius) or absent (some
Claudius, some Dermatemys, Xenochelys), but they are never as large and posteriorly projecting as in the Chelydridae or some of the Emydidae. Reduction of this projecting quality could be a shared derived feature of the Trionychidae. It occurs elsewhere among the Chelonoidae (Chelonia), “Bataguridae” (Malayemys), and Testudinidae (several genera). The absence of a projecting processus is certainly derived for the Trionychidae and possibly for the Trionychidae plus Carettochelys (character 52, table 12).

The elongate basisphenoid of trionychids varies in shape. In most species, as in the outgroups, it has a subtriangular shape although it is usually somewhat more elongate. In a few forms medial constriction of the basisphenoid occurs either occasionally or frequently. The presence of an hourglass shaped basisphenoid is considered derived within the Trionychidae (character 64, table 11).

VARIATION IN THE VISCERAL SKELETON AND NONSHELL POSTCRANIA

Although the nonshell postcranial elements of turtles have been shown to provide valuable systematic data and are important in currently used arrangements, they have not been used extensively. The most important modern studies of the systematic value of nonshell postcrania are found in Williams (1950) and Zug (1971). Williams’ (1950) monograph on the cervical articulations of turtles forms the foundation of the most frequently used modern classifications of turtles (see discussion). Zug (1971) provided data on the pelvic girdle and hind limbs which has since been cited as evidence for the recent realignment of certain cryptodires (Gaffney, 1975, 1984).

In the current attempt to determine the best hypothesis of relationships for trionychids, data from the cervical and thoracic vertebrae, the hyoid, and the pelvic and pectoral girdles have been found to be extremely valuable. Characters of the appendages and caudal vertebrae are of less use. The visceral skeleton has been included with the other nonshell postcrania in an effort to balance the size of the three osteological data sets.

With the exception of the hyoid and the lower jaw, the characters treated in this section are most valuable in determining interfamilial relationships of trionychids. The hyoid and lower jaw are also important at this level but prove to be of additional value in the study of intrafamilial relationships.

MANDIBLE

The lower jaw of trionychids is remarkable for its very high coronoid processes and large retroarticular processes (Boulenger, 1889) and for the significant contribution to the area articularis mandibularis made by the surangular (compare figs. 16 and 17). The retroarticular process is much larger than that of other turtles (except Carettochelys) and adds 10 percent or more to the total length of the jaw (character 99, tables 16, 18).

As observed by Gaffney (1979b), the prearticular and surangular of trionychids are frequently in contact, restricting or subdividing the fossa meckelii (fig. 17, top). In 82 percent (81/98) of the trionychids examined the prearticular and surangular meet either on the posterior edge of the fossa meckelii (36/98) or divide it by meeting across the middle (45/98). There is no clear pattern of variation among the species within the family. All 3 conditions occur in three taxa; 2 of 3 conditions occur in 1 1 others. The high incidence of surangular-prearticular contact across the fossa meckelii could be considered a shared derived feature of the family Trionychidae. However, it occurs in several other taxa and absence of a clear distribution makes this character unusable. In Carettochelys one-half of the specimens (N = 4) examined show this contact. Elsewhere among cryptodires it occurs in some Kinosternon, in Dermatemys, in Platysternon, and in some pleurodires.

In most turtles the area articularis mandibularis is made up by the articular with little or no contribution from the surangular (fig. 16, top). Only in the Trionychidae and Carettochelys does the surangular make up one-half or more of this surface (fig. 17, top). The surangular is always included in this area in other trionychoids but always forms less than half of the articular surface. In testudinoids and chelydrids the surangular is frequently absent from the area articularis mandibularis and when present contributes less
### TABLE 16

Systematic Characters and Character States of the Lower Jaw and Nonshell Postcrania of Trionychid Turtles

<table>
<thead>
<tr>
<th>Character</th>
<th>Character states</th>
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</thead>
<tbody>
<tr>
<td>79. entepicondylar foramen open along humerus</td>
<td>1. no &lt;br&gt; 2. variable &lt;br&gt; 3. yes</td>
</tr>
<tr>
<td>80. hyperphalangy of manus digits 4 and 5, pes digit 4</td>
<td>1. no &lt;br&gt; 2. yes &lt;br&gt; 3. yes</td>
</tr>
<tr>
<td>81. radius and ulna in contact adjacent to manus</td>
<td>1. no &lt;br&gt; 2. yes &lt;br&gt; 3. yes</td>
</tr>
<tr>
<td>82. number of clawed digits of manus</td>
<td>1. 5 &lt;br&gt; 2. 3 or fewer &lt;br&gt; 3. 2 or fewer</td>
</tr>
<tr>
<td>83. cervical centra 2–7 opisthocoels</td>
<td>1. no &lt;br&gt; 2. yes</td>
</tr>
<tr>
<td>84. centra of 8th cervical and 1st body vertebrae in contact</td>
<td>1. yes &lt;br&gt; 2. no</td>
</tr>
<tr>
<td>85. ventral process on 8th cervical</td>
<td>1. present &lt;br&gt; 2. absent</td>
</tr>
<tr>
<td>86. ventral process on 8th cervical</td>
<td>1. single &lt;br&gt; 2. double</td>
</tr>
<tr>
<td>87. ventral keel on 8th cervical present and limited to posterior end</td>
<td>1. no &lt;br&gt; 2. yes</td>
</tr>
<tr>
<td>88. strong dorsal processes on cervicals</td>
<td>1. no &lt;br&gt; 2. yes</td>
</tr>
<tr>
<td>89. number of posterior body vertebrae with transverse processes not reaching pleurals</td>
<td>1. 0 &lt;br&gt; 2. 1 &lt;br&gt; 3. 2</td>
</tr>
<tr>
<td>90. number of ossifications in corpus hyoidis</td>
<td>1. 1 &lt;br&gt; 2. 6 &lt;br&gt; 3. 9</td>
</tr>
<tr>
<td>91. number of ossifications in corne branchiæ II</td>
<td>1. 1 only &lt;br&gt; 2. 2–6 &lt;br&gt; 3. 7 or more</td>
</tr>
<tr>
<td>92. ossifications of corne branchiæ II broad and strongly tutured</td>
<td>1. no &lt;br&gt; 2. yes</td>
</tr>
<tr>
<td>93. basiroyals in close contact and projecting anteriorly</td>
<td>1. no &lt;br&gt; 2. yes</td>
</tr>
<tr>
<td>94. surangular forms part of area articularis mandibularis</td>
<td>1. less than ½ &lt;br&gt; 2. less than ½ &lt;br&gt; 3. greater than or equal to ½</td>
</tr>
<tr>
<td>95. symphyseal ridge strong and present in a depression</td>
<td>1. no &lt;br&gt; 2. yes</td>
</tr>
<tr>
<td>96. foramen nervi auriculotemporalis with two lateral openings</td>
<td>1. no &lt;br&gt; 2. yes</td>
</tr>
</tbody>
</table>

than half the articular area. The large contribution by the surangular in trionychids must be considered derived. The condition in other trionychoids appears to be intermediate between the state in the Trionychidae and that in other turtles (character 94, table 18).

An important systematic character in the lower jaw of trionychids is the presence of a

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**TABLE 16—(Continued)**

<table>
<thead>
<tr>
<th>Characters</th>
<th>Character states</th>
</tr>
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<tbody>
<tr>
<td>97. foramen nervi auriculotemporalis with one lateral and one dorsal opening</td>
<td>1. no &lt;br&gt; 2. yes</td>
</tr>
<tr>
<td>98. foramen intermandibularis caudalis enclosed by prearticular</td>
<td>1. sometimes &lt;br&gt; 2. never</td>
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<tr>
<td>99. retroarticular process large, about one-tenth of total lower jaw</td>
<td>1. no &lt;br&gt; 2. yes</td>
</tr>
<tr>
<td>100. ilia curve medially</td>
<td>1. no &lt;br&gt; 2. yes</td>
</tr>
<tr>
<td>101. ilia curve posteriorly</td>
<td>1. no &lt;br&gt; 2. yes</td>
</tr>
<tr>
<td>102. ilia anteroposteriorly expanded at distal end</td>
<td>1. yes &lt;br&gt; 2. no</td>
</tr>
<tr>
<td>103. thelial process present</td>
<td>1. no &lt;br&gt; 2. yes</td>
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<tr>
<td>104. pubis and ischiium closely opposed or in contact across thyroid fenestra</td>
<td>1. no &lt;br&gt; 2. yes</td>
</tr>
<tr>
<td>105. epipubic region ossifies</td>
<td>1. yes &lt;br&gt; 2. no</td>
</tr>
<tr>
<td>106. pectineal processes and interpubic suture lie in a single plane</td>
<td>1. no &lt;br&gt; 2. yes</td>
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<tr>
<td>107. ischia extend into thyroid fenestra</td>
<td>1. yes &lt;br&gt; 2. no</td>
</tr>
<tr>
<td>108. pectineal processes equal to or wider than interpubic contact</td>
<td>1. no &lt;br&gt; 2. yes</td>
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<tr>
<td>109. metischial processes present and distinct</td>
<td>1. yes &lt;br&gt; 2. no</td>
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<tr>
<td>110. iliischial notch</td>
<td>1. absent &lt;br&gt; 2. present</td>
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<tr>
<td>111. coracoid shortest of three pectoral processes</td>
<td>1. no &lt;br&gt; 2. yes</td>
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<tr>
<td>112. angle of acromion process to scapula approaches that of coracoid to acromion</td>
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<tr>
<td>113. coracoid longest of three pectoral processes</td>
<td>1. no &lt;br&gt; 2. yes</td>
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TABLE 17
States for Characters Found to be Useful in Hypothesizing Relationships Among Recent Trionychid Turtles

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</table>

*See table 16 for explanation of characters and character states.

sagittal ridge on the triturating surface at the symphysis (De Broin, 1977). This ridge usually forms within a depression on an otherwise flat surface (fig. 17, top). Such a single ridge does not occur in other turtles and appears to be derived within the Trionychidae. Among the members of this family a ridge occurs only in the Indian species, and in *Trionyx cartilagineus* and *T. formosus* (character 95, table 17). A ridge is also present in the largest individuals of *T. subplanus*.

The foramen nervi auricolotemporalis is a single or multiple opening in the surangular ventral to the area articulares mandibularis. Gaffney (1979b) reported multiple openings for this foramen only in *Podocnemis expansa*. Two or more lateral openings are also present in some specimens of almost every species of trionychid. Additional pleurodires (*Pelusios castaneus*) and also some testudinoids (*Cuora, Graptemys, and Gecclemy*) also have multiple lateral openings in the surangular. The occurrence of multiple lateral openings in the surangular, representing a divided foramen nervi auricolotemporalis, is considered derived (character 96, table 18).

Gaffney (1979b) mentioned an additional, apparently unnamed, foramen in the surangular that communicates with the foramen nervi auricolotemporalis and the fossa meckeli. Unlike the foramen nervi auricolotemporalis, it opens dorsally, not laterally. It is mentioned as occurring in *Staurotypus* and *Terrapene*. I have noted this opening in all kinosternids examined, and in *Platysternon*, but in no other taxa. The occurrence of the opening can clearly be considered derived and it appears to be a shared derived character for the Kinosternidae (character 97, table 18).

On the lingual surface of the jaw, in the suture between the prearticular and the angular, there may appear two foramina, the foramina intermandibularis oralis and caudalis (fig. 16, bottom). In most turtles there is evidence of both. In trionychids the anterior one (oralis) is never present and the pos-
terior one (caudalis) may be present or absent in some species, but is always absent in others (character 98, table 17). This uniform absence of the foramen intermandibularis caudalis is considered to be derived within the Trionychidae.

**HYOID**

The hyoid of most cryptodires is not an elaborate structure. It typically consists of a single basal unit, the corpus hyoidis, which may or may not be ossified, and two pairs of branchial horns, cornu branchiale I and II, the anterior pair of which is always ossified (fig. 18A). By contrast, the hyoid of trionychids always consists of a minimum of ten ossifications and may include as many as 40 (fig. 18B–F). The corpus hyoidis is composed of either three pairs of ossifications (one pair of basihyals and two pairs of basibranchials, fig. 18B, E), or four pairs of ossifications (an additional pair is present anterior to the basihyals, fig. 18C, D, F). Cornu branchiale I always consists of a single ossification while cornu branchiale II consists of 1 to 18 ossifications.

Ossification of the corpus hyoidis from numerous centers has been recognized as a unique feature of the Trionychidae (Siebenrock, 1913; Romer, 1956) (character 90, table 18). This highly developed structure is also known to vary among the species of the Trionychidae (Annandale, 1912; Siebenrock, 1913), and characters of the hyoid appear to be useful in assessing intrafamilial relationships.

Most members of the Trionychidae have...
Fig. 17. Lower jaw of Trionyx cartilagineus (RH 129). Top, dorsal view, bottom, medial view of right ramus. Abbreviations are same as for figure 16.

six ossifications of the corpus hyoidis throughout life. However, in eight species the corpus has six ossifications in subadults but a total of eight ossifications at full maturity (character 90, table 17). This exceptionally high number in these select species is considered to be a further derived state.

Cornu branchiale I is a single ossification in all adult cryptodires examined in the course of this study. Cornu branchiale II, when ossified, also consists of a single element, except in some trionychids. In all of the Cyclanorbinae (fig. 18B) and in most Trionyx hurum (fig. 18C) it ossifies from a single center. In the remainder, it ossifies from as few as 2 to as many as 18 centers. Interspecific variability in the number of centers of ossification in cornu branchiale II falls into two seemingly natural groups with two exceptions. In most Old World forms the second horn includes six or fewer ossifications (fig. 18C–E). Only among living New World species and T. euphraticus does it always consist of seven or more (fig. 18F; character 91, table 17). In T. gangeticus it consists of 5 to 14 centers ($\bar{x} = 8.4$) and in T. sinensis it consists of 3 to 9 centers ($\bar{x} = 5.1$). These two species are assigned to a group based on their average number of ossifications. As is the case for the corpus hyoidis, a high number of ossifications in cornu branchiale II is considered derived.

In Chitra indica and Pelochelys bibroni, cornu branchiale II consists of three ossifications which are very broad and strongly sutured to one another (fig. 18D). This is a unique condition within the Trionychidae (character 92, table 17).

The corpus hyoidis of cyclanorbine trionychids can always be recognized by the close
### TABLE 18

**Distribution of the States of Characters of the Mandible and Non-shell Postcrania Used to Develop a Hypothesis of Relationship of the Trionychidae to Other Turtles**

| Characters | 79 | 80 | 81 | 82 | 83 | 84 | 85 | 86 | 87 | 88 | 89 | 90 | 91 | 92 | 93 | 94 | 95 | 96 | 97 | 98 | 99 | 100 | 101 | 102 | 103 | 104 | 105 | 106 | 107 | 108 | 109 | 110 | 111 | 112 | 113 |
|------------|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|
| Trionychidae | 3 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | - | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 |
| Carettochelys | 1 | 1 | 2 | 3 | 2 | 1 | 1 | 2 | 2 | 3 | 1 | 1 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 |
| Cladus | 3 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 3 | 2 | 1 | 2 | 1 | 1 | 2 | 2 | 1 | 1 | 2 | 1 | 2 | 1 | 2 | 1 | 2 | 1 | 2 | 1 | 2 | 1 | 2 | 1 |
| Stauropterus | 3 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 3 | 2 | 1 | 2 | 2 | 2 | 1 | 2 | 2 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 1 | 2 | 1 | 1 | 2 | 1 | 2 | 1 |
| Kinosternidae | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 3 | 1 | 2 | 1 | 2 | 2 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| Dermatemydidae | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 3 | 1 | 2 | 1 | 2 | 2 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| Cheydridae | 2 | 1 | 2 | 3 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| Emydidae | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| Testudinidae | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| Neurodina | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |

* See table 16 for explanation of characters and character states. Characters marked with an asterisk are variable (see table 17).

As early as 1876 it was recognized that the members of the Trionychidae had unique cervical articulations (Williams, 1876). The cervical series continues to be used as strong evidence for monophyly of the Trionychidae (Boulenger, 1894; Siebenrock, 1902; Loveridge and Williams, 1957). In both families all cervicals are opisthocoelous (character 83, table 18) except for the eighth in trionychids, which has no central contact to the first thoracic vertebra (character 84, table 18). The members of the Trionychidae are also unique in having no ventral process on the eighth cervical (Williams, 1950). The double ventral process found in the eighth cervical of all other cryptodires (fig. 19C, D) is considered to be derived but lost in the Trionychidae (character 85, table 18). The mechanism described by Dalrymple (1979) for the eighth cervical can be derived only in trionychids (character 86, table 18).
dorsal processes on the middle to posterior cervical vertebrae (fig. 20). The presence of these processes is considered derived (character 88, table 17).
Fig. 19. Ventral view of the eighth cervical vertebra of four eucryptodiran turtles. A. Trachemys scripta (AMNH 111961); B. Trionyx ferox (AMNH 129737); C. Staurotypus triporcatus (83-JI-202); D. Carettochelys insculpta (UF 43823).

Chelonia have 10 thoracic vertebrae between the cervicals and the sacrals, and they normally have 8 pairs of pleural bones. Thus, two thoracic vertebrae are not associated with a pair of pleurals. One of these is the first body vertebra. It sends transverse processes posterolaterally to join the anterior edge of the ribs associated with the first pair of pleurals (fig. 6). The other vertebra which is without associated pleurals is the tenth. The tenth thoracic vertebra may be firmly fixed by transverse processes which brace it against a tuberosity on the eighth pleural (fig. 6A), or it may be somewhat less well fixed and have only remnants of transverse processes (fig. 6B, C; Zug, 1971). In the Kinosternidae the ninth thoracic vertebra is like the tenth in having no contact between the transverse processes and the carapace. In this family both the ninth and tenth vertebrae exhibit some freedom of movement.

The distribution among all turtles of these three conditions of the posterior thoracic vertebrae (character 89, table 18), suggests that reduced articulation between the shell and these posterior vertebrae is derived.

Fig. 20. Lateral views of the sixth cervical vertebrae of two trionychid turtles. A. Cycloderma aubryi (MRAC 19212); B. Trionyx ferox (AMNH 129737). Anterior is to the right.

PELVIS

Numerous features of the trionychid pelvic girdle are useful in phylogenetic analysis. There are no fewer than 10 characters which are germane to establishing interfamilial relationships. Three of these are used in the intrafamilial analysis as well. The pelvic girdle is treated as follows: ilium first, and then puboischiatic plate from anterior to posterior.

The ilia in most turtles extend dorsally from the acetabulum to meet the carapace and transverse processes of the sacral vertebrae. The main axis of the ilium is straight in all turtles except trionychids (Zug, 1971). In trionychids they are strongly flexed posteriorly (character 101, table 18). Zug (1971) indicated that these posteriorly curved ilia do not articulate with the carapace in trionychids. This is certainly the case in all trionychine trionychids, but carapacial contact does occur in some cyclanorbines (see discussion of shell character 21).

Hirayama (1985) has suggested that lateral
curvature of the ilia is a feature unique to the Testudinoidea. I believe he means medial curvature because I find medially curved ilia in all testudinoids examined. In numerous trionychoids including some trionychids (character 100, table 17), Carettochelys, Dermatemys, and most kinosternids (character 100, table 18) the ilia are also medially curved. The character state is therefore shared by all of Gaffney’s (1984) Chelomacryptodira (Trionychoidea plus Testudinoidea). Its absence in most trionychids can be considered a loss of the condition, and thus derived within the family.

The dorsal end of the ilium of all turtles except trionychids and smaller kinosternines is anterioposteriorly expanded. This distal sagittal crest is the site where the transverse processes of the sacral vertebrae articulate. Based on a single individual, Zug (1971) described the distal end of the ilium of Dermatemys as being unexpanded. In four Dermatemys and in three Carettochelys (not examined by Zug) available for this study the distal ilia are anteroposteriorly expanded. The absence of this distal expansion is considered derived (character 102, table 18).

The thelial process, site of attachment for the iliotibialis muscle, has been considered to be a unique feature of the Kinosternidae (Zug, 1971). A topographically and morphologically similar structure occurs on the ilium of all three Carettochelys pelves available to me (fig. 21B, D). In addition, a small tubercle, in the position of the thelial process, is present in three of six individuals of Lissemys punctata examined (fig. 21E). The presence of a thelial process is considered to be derived for kinosternids and Carettochelys (character 103, table 18).

The epipubis is a small plate of cartilage or bone which extends anteriorly in a horizontal plane from the region of the pubic symphysis (fig. 21A, B). Hay (1908) has suggested that an unossified epipubis is primitive for turtles. Although it is the last center in the pelvic girdle to ossify it does ossify in all cryptodires except the most derived trionychoids (the Caretochelyidae and Trionychidae, fig. 21C–F), most cheloniids (Baur, 1891a, reports that some old cheloniids ossify the epipubis), and testudinids. The lack of ossification of the epipubis appears to be a derived and possibly paedomorphic feature (character 105, table 18).

The pectineal processes extend from the body of the pubis in an anterior or anterolateral direction. In most cryptodires they are small relative to the length of interpubic contacts (fig. 21A, B, D). The members of the Trionychidae are unique in having pectineal processes which are as wide as or wider than the length of interpubic contact (fig. 21C, E, F; character 108, table 18).

The pectineal processes and the interpubic symphysis of trionychids lie in a single plane and they all lie flat against the plastron (Zug, 1971). In nearly all other cryptodires no such common plane exists. The exceptions are living chelonioïds and Cladius, but in these taxa the anterior pubic region does not lie flat on the plastron. In skeletons of very young specimens of Kinosternon and Sternotherus the entire pubis is quite flat. It appears that the pelvis first ossifies in a single plane and with age gains three-dimensional qualities. Thus the occurrence of a flat pubis in trionychids may be a retention of the juvenile state (character 106, table 18).

The thyroid fenestra is the major opening in the puboischiatic plate. In turtles it is often partially or completely divided by bone (fig. 21A). Bony division occurs in two nonhomologous ways: by ossification of the median gastroid cartilage or by junction of medial extensions of the pubes and ischia (Walker, 1973).

A divided thyroid fenestra is the common condition among Recent turtles (character 104, table 18; Baur, 1891a; Zug, 1971). But the bony junction in chelydrids and Dermatemys occurs through ossification of the medial gastroid cartilage, a structure which is found in all open forms (Baur, 1891a). This is a minor modification of an otherwise completely open condition. Very distinct reduction and division of the thyroid fenestra occurs by extention of the pubis and ischium into the fenestra. Among living cryptodires this occurs only in Platysternon, kinosternine kinosternids, and testudinoids.

Baur’s (1891a) interpretation of this character is that an open thyroid fenestra is primitive and a divided fenestra derived. Data from living turtles support this hypothesis. However, Proganochelys (Gaffney, ms), some
Fig. 21. Dorsal views of the pelvis of six eucryptodiran turtles. A. *Pseudemys nelsoni* (AMNH 129736); B. *Staurotypus triporatus* (UF 13482); C. *Trionyx ferox* (AMNH 129737); D. *Carettochelys insculpta* (AMNH 84212); E. *Lissemys punctata* (UF 56017); F. *Chitra indica* (FMNH 224228). Abbreviations: il, ilium; isch, ischium; pub, pubis. Stippled areas represent calcified cartilage.
chelonioids, and some baenids (Hay, 1908) have the thyroid fenestra divided by ischiopubic contact. If the divided condition is found among other extinct families, the use of global parsimony may require this state to be recognized as primitive. Should this be the case, then an open foramen could be used as a shared derived character within the Chelydidae, the Chelonioidea, and Trionychoidea. For the present, Baur’s interpretation is accepted.

Baur (1891a) indicated that expansion of the undivided thyroid fenestra in trionychids is a uniquely derived condition. This fenestra is open widely, and ischial extension into it is minimal (Dermatemys and staurotypines, fig. 21B) or absent (most trionychids and Carettochelys, fig. 21D–F) in all trionychoids except for kinosternines. When the ischia do extend into the thyroid fenestra in species of the Trionychidae (fig. 21E), this is considered to occur by reversal to the primitive condition. It appears only in Lissemys punctata, Cycloderma aubryi, and C. frenatum (character 107, table 17).

Most trionychids, and in fact most cryptodires, have distinct, posteriorly directed processes of the ischia, the metischial processes (fig. 21A, D, F). In seven species of trionychids (all five living species of the Cyclanorbinae, Trionyx euphraticus, and T. ferrox) these processes exist only as posteromedial expansions of the ischia and not as free projections (fig. 21C, E). Outgroup taxa which also lack metischial processes include Claudius, Staurotypus (fig. 21B), some Kinosternon, some Dermatemys, and some cheloniids. Because metischial processes are present in Carettochelys (the proposed sister group for the Trionychidae), some members of the other two trionychoid families and most other turtles, their presence is judged to be primitive for the Trionychidae and their absence derived (character 109, tables 17, 18).

One additional character of the pelvis, which bears on the current problem only in that it supports monophyly of the Kinosternidae, is a distinct notch in the acetabulum at the junction of the ilium and ischium (fig. 21B). Such a notch is present in Staurotypus, Claudius, and most Kinosternon (character 110, table 18).

Pectoral Girdle

The pectoral girdle of all turtles is a triradiate structure composed of two elements, the scapula and coracoid. From the acetabulum the main body of the scapula extends dorsomedially to the carapace in the region of the first body vertebra. The acromion process of the scapula extends anteromedially to the plastron. The coracoid joins the scapula only at the glenoid fossa and projects posteriorly toward the midline of the plastron. The relative lengths of these three projections and the angles between them vary in a systematically useful manner. Their use in systematics up to this time appears to be limited (Meylan and Auffenberg, 1986).

In most turtles, the dorsal projection of the scapula is the longest of the three pectoral processes. The only exceptions are the chelonioids, trionychine trionychids, and Carettochelys in which the coracoid is longer (character 113, tables 17, 18). The shortest projection is the acromion process of the scapula except in the Testudinoidea in which the coracoid is always shortest (character 111, table 17). An exceptionally long or exceptionally short coracoid is considered to be derived.

Two angles in the pectoral girdle, one between the acromion process and main body of the scapula and the other between the acromion process and the coracoid, were measured. In most cryptodires the former angle approaches 90° and is always much greater than the latter. The same is true for majority of trionychids although the larger angle tends to be somewhat less (65–75°). In six taxa the acromion-scapula angle is lower still and the coracoid-acromion angle is higher, so that there is little or no difference between them. The similarity of these two angles is considered to be a derived character state within the Trionychidae (character 112, table 17).

Appendicular Skeleton

The humerus and femur of trionychids are remarkably similar in general appearance. Both form gentle S-shaped curves, both have two large proximal trochanters which are free from each other, and both have weakly differentiated distal tubercles. The humerus can
be distinguished from the femur most easily by the presence of an entepicondylar groove that is always open in this family. Furthermore, the lesser trochanter of the humerus lies in an anteroposterior plane that runs through the main axis of the humerus. The greater trochanter of the humerus and both trochanters of the femur lie at a high angle to this plane.

The condition of the entepicondylar foramen of the humerus is constant in the Tri-onychidae, but it can be open or closed in pleurodires, Kinosternon, Dermatemys, and among the various genera of emydids. It closes with age in chelydrids, and is apparently always open in Carettochelys. It is always open in chelonids and staurotypines. Because the closed condition is found in some members of all three outgroup trionychoid families, the consistently open condition in the Trionychidae is unique within the superfamily (character 79, table 18).

The carpus and tarsus of trionychids do not differ significantly from those of other cryptodires (Hay, 1908; Ogushi, 1911). The carpus consists of ten elements: an intermedium, ulnare, and pisiform, two centralia, and five carpals. Unlike most other turtles, the trionychids do not have the intermedium separating the distal ends of the radius and ulna; instead these forearm elements have a strong contact. The only other taxa in which this occurs are the families Cheloniidae and Testudinidae (character 81, table 18).

Among trionychids there is a uniform number of phalanges in digits one, two, and three (those which are clawed) but a variable number in digits four and five. The most common phalangeal formula for turtles is 2-3-3-3-3 (Romer, 1956). In those digits of trionychids which are clawed, 1, 2, and 3 have this number. Those which have no claws (digits 4 and 5) may differ from this most common, and according to Hay (1908), primitive number. In almost every trionychid for which an articulated manus is available the fourth digit has at least four phalanges, a few have five, and Lissemys and Chitra have as many as six. Only Cyclanorbis senegalensis (one specimen available) appears to retain the primitive number of three elements. Despite this exception, hyperphalangy of the fourth digit is considered to be a derived feature of the Trionychidae. Hyperphalangy of the fifth digit of the manus is less common in the Trionychidae. Although there is some interspecific variation within the data set for both of these characters, the data are not sufficient to allow use of this character in the intrafamilial analysis.

Hyperphalangy of the fourth digit of the pes is also commonplace for trionychids. There is variation among family members but, like the manus, the data are insufficient to include them in the analysis of intrafamilial relationships. Hyperphalangy is treated as a single character (character 80, table 18) and is used only in the interfamilial analyses.

DISCUSSION

HIGHER RELATIONSHIPS OF THE TRIONYCHIDAE

MONOPHYLY OF THE TRIONYCHOIDEA

The characters examined during the course of this study support the hypothesis that the families Dermatemyidae, Kinosternidae, Carettochelyidae, and Trionychidae form a monophyletic group. These relationships were suggested by Gaffney (1975) who assembled these families as the superfamily Trionychoidea (fig. 22). Relationship of the Trionychidae to the Kinosternidae and Dermatemyidae was first proposed late in the last century by Baur (1891a). Although it has subsequently been supported by the work of Albrecht (1967), Zug (1966, 1972), and Gaffney (1975, 1979b, 1984), it is not frequently cited (an exception is Smith and Smith, 1980). An alternative proposal for the higher relationships of turtles by Williams (1950, reproduced here as fig. 23) has received wider use (Dowling and Duellman, 1974; Goin and Goin, 1962, 1971; Porter, 1972; Pritchard,
TABLE 19

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<th>Character code</th>
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<tr>
<td>26</td>
<td>at least one pair of plastral buttresses fails to reach pleurals</td>
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<tr>
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<td>cheek emargination reduced</td>
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<td>palatines contribute significantly to braincase</td>
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<td>55</td>
<td>basis tuberculi basalis absent</td>
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<td>57</td>
<td>canalis carotici straight and wide</td>
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<td>no groove for stapedial artery on prootic or parietal</td>
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<td>77</td>
<td>quadrate contribution to processus troclearis oticum less than 50%</td>
</tr>
<tr>
<td>94</td>
<td>surangular always present in area articularis mandibularis</td>
</tr>
<tr>
<td>89</td>
<td>transverse processes of tenth body vertebra do not articulate with carapace</td>
</tr>
</tbody>
</table>

1979a, 1979b; Romer, 1956, 1966; Wermuth and Mertens, 1961; Zug, 1966). The Williams arrangement places the family Trionychidae alone in the superfamily Trionychoidea. The Kinosternidae (as the Kinosterninae and Staurotypinae) is included in the Chelydridae which, along with the Dermatemydidae, is considered part of the Testudinoidea (fig. 23). The Carettochelyidae is confined to its own superfamily, the Carettochelyoidea.

Gaffney (1984) summarized the evidence for using the superfamily Trionychoidea (sensu Gaffney, 1975) which until now consisted largely of characters of the cranial arteries. Additional characters of the skull, lower jaw, shell, and body vertebrae are here shown to support this inclusive view of the Trionychoidea (table 19) as the most parsimonious hypothesis for relationships among living eucryptodires. Furthermore, the criteria which Williams (1950) used to include the Kinosternidae in the Testudinoidea are shown to be plesiomorphic or subject to homoplasy.

A critical feature of Gaffney’s (1975, 1984) definition of the Trionychoidea is the inclusion of the Carettochelyidae. Previously, the carettochelyids had been thought of alternatively as pleurodires (Boulenger, 1889), as the missing link between trionychids and chelonioi (Strauch, 1890), or as a link between dermatemydids and kinosternids, and the Trionychidae (Baur, 1891a; Gaffney, 1975; and others). It is abundantly clear from the present analysis that the last of these three alternatives is the one best supported by available data.

Although the present study has not reexamined characters of the cranial arteries (McDowell, 1961; Albrecht, 1967; and Gaffney, 1975, 1979b, 1984), two of the external skull characters examined do reflect the different arterial patterns that distinguish trionychoids from other cryptodires. The small size of the stapedial artery in trionychoids is reflected by the absence of any grooves or furrows to accommodate this vessel where it crosses the prootic and the descending process of the parietal (character 61). In chelidrids, emydids, and testudinids, by contrast, there is a distinct though variably developed furrow or groove for the stapedial artery. In certain taxa (Chelydra, Melanochelys, Terrapene) these grooves extend for long distances. In other forms, especially testudinids, they are short but deep and found only adjacent to the foramen stapediotemporale.

The second arterial feature noted here re-
Fig. 23. A cladogram of the Testudines based on the classification in Williams (1950).

Reflects the increased importance of the internal carotid artery in Recent trionychoid skulls. In this superfamily, a stiff wire of a diameter just less than the foramen posterior canalis carotici interni, will pass easily from this foramen through the foramen anterior canalis carotici interni, and into the braincase (character 57). This is possible because the canalis carotici follows a very straight path. In other living cryptodires the path followed by the internal carotid artery is less direct as can be seen in figures 26-29 in Gaffney (1979b).

A useful feature of the skull used by Gaffney (1975), which does not involve blood flow pattern is the inclusion of the palatine in the lateral wall of the braincase. In essentially all turtles other than trionychoids, palatine participation is insignificant or absent (character 43) (Morenia and Hardella have a strong palatine contribution to the braincase wall, McDowell, personal commun.). In trionychoids it is quite extensive, often extending posteriorly nearly to the foramen nervi trigemini (fig. 13).

There are three additional features of the trionychoid skull which can be added to the evidence for monophyly. The cheek is solid (little cheek emargination, character 39); the dorsal surface of the basioccipital is smooth (no basis tuberculi basalis, character 55); and less than one-third of the processus trochlearis oticum is made up by the quadrate (character 77).

Among living turtles only living chelonioinds (Cheloniidae, Dermochelyidae) and Platysternon share with the trionychoids such
limited cheek emargination. In none of these taxa does it extend above the lower rim of the orbit. Well-developed cheek emargination in the Pleurodira, baenids, pleisochelyids, and most chelydrids suggests that its absence in the Chelonioida and Trionychoida is derived.

The basioccipital is without a basis tuberculi basalis in certain cryptodires and may be most easily explained as a single loss in the Trionychoida and a single loss in the advanced Testudinoidea (Rhinoclemmys and the Testudinidae, except Gopherus). The small quadratojugal contribution to the processus trochlearis oticum also occurs in two separate monophyletic groups, the chelonioids and the trionychoids.

A single character of the lower jaw lends support to the argument for monophyly of the Trionychoida. Throughout the superfamly there is always contribution by the surangular to the area articularis mandibularis (character 94). In certain forms it makes up the majority of this surface; in others it makes up a smaller part. It is never absent from this area, as in some testudinoids and chelydrids.

Absence of pleural contact by one or both plastral buttresses is a useful feature of the shell of trionychoids (character 26). The presence of two pairs of well-developed buttresses in the Pleurodira, Plesiochelyidae, Baenidae, and testudinoids is used here as evidence that they were present in primitive cryptodires and that absence of one or both pleural contacts can be considered derived for chelydrids, chelonioids, and trionychoids. Even if absence of plastral buttresses were the primitive condition for cryptodires, the character is still a very useful one. Testudinoids could then be recognized as having two pairs of well-developed plastral buttresses except for the most kinetic forms (Cuora, Terrapene). No trionychoid taxa could be included in such a group.

An important character of the posterior thoracic vertebrae is used here as evidence of monophyly of the Trionychoida. As mentioned by Zug (1971), the tenth body vertebra, which is immediately anterior to the sacral pair, lacks contact of its transverse processes to the pleurals in members of this superfamily (fig. 6B, C). This condition occurs also in Recent chelonioids, testudinoids, and Platysternon (character 89). In Chelydra and Macrochelys this character is variable. If the presence of free transverse processes of the tenth body vertebra is actually primitive, then this character would be equivalent to the alternative possibility given for the plastral buttresses above. That is, complete tenth transverse processes would be derived for the Chelonioida and Testudinoidea and this would exclude any trionychoids from either of these superfamilies.

In summary, there are seven osteological characters, in addition to the two that correlate with cranial circulation patterns, that suggest that the Trionychoida (sensu Gaffney, 1975) is monophyletic. The most commonly cited alternative, which places the Dermatemyidae and Kinosternidae along with the Chelydridae in the Testudinoidea, requires that all nine characters used here occur twice, once in the Trionychoida and once in the Testudinoidea.

Observations on the morphology of the cloacal region support monophyly of the Trionychoida. In all four families cloacal bursae are absent (Smith and James, 1958). This can be cited as additional evidence with the assumption that absence in trionychids occurs independently of absence in chelonioids and testudinids. Also, the penis in all four families of the Trionychoida has a singly or doubly bifurcate seminal groove (Zug, 1966), a condition that occurs elsewhere only in the Testudinidae.

The evidence presented by Williams (1950) for including the Kinosternidae (as the Kinosterninae and Staurotypinae) within the Chelydridae consists of two plesiomorphic characters, and three highly variable characters. The existence of costiform processes of the nuchal is widespread among cryptodires and is most clearly visible in hatchlings and juveniles. Their retention in adults could be considered a shared derived character of the chelydrids and kinosternids, but they are also retained in adult Dermochelys, Dermatemys, and trionychids. Their presence is probably primitive for the Cryptodira.

The evidence from the cervical formula is similarly of little value. The presence of a single biconvex vertebra and a doubly procoelous eighth cervical is used by Williams...
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(1950) as evidence of relationship of chely-
drids and kinosternids. But these features are
also present in chelonioïds and dermately-
dids which suggests that they are actually
primitive for euctepthodié. Independent
modification of this cervical formula sup-
ports monophyly of the Testudinoidea (usu-
ally two biconvex cervicals in the cervical
series) and the Carettochelyidae plus Trio-
nychidae (no biconvex cervicals, numbers two
through seven opisthocoelous).

Williams (1950) cited a variable number
of marginal scales, 23 or 25, as a character
of his Chelydridae. The number of marginal
scales reflects variation in the number of pe-
ripheral bones (Hutchison and Bramble,
1981). The Williams arrangement would re-
quire that reduction in the number of pe-
ripheral bones from 22 to 20 occur twice,
one in his Testudinoidea and once in his
Carettochelyoidea. In the arrangement ad-
vocated here this can be treated as a single
event and as part of a transformation series
which culminates in complete loss of periph-
erals in the Trionychidae.

Broad unridged alveolar surfaces occur in
numerous unrelated taxa in addition to those
included in Williams' Chelydridae. They ap-
parently correlate with a durophagous diet
(Pritchard, 1984) and do not constitute strong
evidence of common ancestry of kinosternids
and chelydrids. The cruciform plastron is a
similarly variable character being absent
within Williams' Chelydridae (many Kino-
sternon species) and present outside of this
family (certain trionychoine trionychids and
extinct carettochelyids). There is no strong
case for including the Kinosternidae within
the Chelydridae on osteological grounds.

Bickham and Carr (1983) suggested that
the staurotypines are the sister group of the
Testudinoidea (in which they include Platys-
 sternon), which supports the Williams (1950)
arrangement in part. These authors rely on
the recognition of a homologous derived
chromosome in the Staurotypinae, Emydi-
dae, and Testudinidae. The crux of their ar-
gument is that the same microsome is fused
to the same identifiable acrocentric macro-
some in these three taxa. However, the com-
bined microsome is euchromatic and ho-
ology of the short arm of their biarmed
second group B macrosome seems tentative
at best (see King, 1985). It is clear that their
results are in irreconcilable conflict with the
morphological evidence. Their observation
that the Trionychioidea and Carettochelyidae
have been separated from the Dermatemy-
didae and Kinosternidae "for a long period of
time" has no bearing on the cladistic re-
lationships of these families.

The data examined in the current study
support alliance of the Kinosternidae and
Staurotypinae with the other trionychids as
suggested by Baur (1891a) and advocated by
Gaffney and others. Additional characters
which indirectly indicate monophyly of the
Trionychioidea (sensu Gaffney) are shared by
members of the Kinosternidae, Carettoche-
lyidae, and Trionychidae. But these charac-
ters suggest an alternative to the dichotomous
view of the Trionychioidea used in Gaffney
(1975, 1984) and shown in figure 24A.
Fig. 24. Three alternative cladograms for the Trionychoidea. The distribution of character states for the numbered nodes is as follows: Node 1: — 26(2) one pair of plastral buttresses reaching pleurals, — 39(2) cheek emargination does not extend above ventral edge of orbit (occurs also in cheloniids, Platysternon, and Malayemys), — 43(2) palatine forms a significant part of the lateral wall of the braincase, — 55(2) basis tuberculi basalis absent (also absent in some batagurines and testudinids), — 57(2) canalis caroticus interni straight and wide, — 61(2) no groove for stapedial artery present on parietal (also absent in some cheloniids), — 77(2) quadrate makes up less than one-half of processus trochlearis oticum (occurs also in chelonoids), — 89(2) transverse processes of tenth body vertebra do not reach pleurals (occurs in some chelydrids), — 94(2) surangular forms up to one-half of area articularis mandibularis. Node 2: — foramen stapedio-temporale reduced or absent, — absence of wave-form or pedicillate sculpturing of shell surface, — enlarged palatine artery and foramen caroticum laterale. Node 3: — 5(2) total number of peripherals 20 or fewer, — 26(3) no plastral buttresses reach pleurals (occurs also in cheloniids and chelydrids), — 86(2) ventral process on eighth cervical double (lost in trionychids which have no ventral process on eighth cervical), — 89(3) transverse processes of body vertebrae 9 and 10 do not reach pleurals (reversed in Carettochelyidae and Trionychidae in which only tenth fails to reach pleurals), — 97(2) foramen nervi auricolotemporalis with one lateral and one dorsal opening (reversed in Carettochelyidae and Tri- onychidae), — 103(2) taenia process present, — 110(2) ilioischial notch present (lost in Carettochelyidae and Trionychidae). Node 4: — 47(2) foramen intermaxillaris present, — 107(2) ischia do not extend into thyroid fenestra of pelvic girdle. Node 5: Characters unique to the Carettochelyidae and Trionychidae: — 28(2) ribheads strongly sutured to vertebral centra, — 30(2) shell sculptured and lacking epidermal scutes, — 44(2) premaxillae fused, — 46(2) basisphenoid contacts palatines, — 50(3) vomer never in contact with pterygoids, — 56(2) foramen posterior canalis caroticus interni completely surrounded by pterygoid, — 83(2) cervicals 2 through 7 ophisthocoeus, — 94(3) 50 percent or more of area articularis mandibularis is formed by surangular, — 99(2) retroarticular process forms about one-tenth of mandible length. Characters of the Carettochelyidae and Trionychidae which also appear in some or all living cheloniids: — 6(2) peripherals never sutured to pleurals, — 52(2) processus pterygoideus externus does not project laterally, — 81(2) radius and ulna in contact adjacent to manus, — 82(2) clawed digits of manus three or fewer, — 105(2) epipubic region never ossifies, — 113(2) coracoid longest of three pectoral processes. Characters of the Carettochelyidae and Trionychidae also found in testudinids and some chelydrids: — 37(2) incisura columella auris closed. Characters of Carettochelyidae and Trionychidae which must be reversals in cladogram presented in figure 24C: — 89(2) only the tenth body vertebra with transverse processes which do not reach the pleurals, — 97(1) foramen nervi auricolotemporalis with both openings lateral, — 110(1) ilio-ischial notch lost.
(1) the Trionychidae and Carettochelyidae share a unique common ancestor; (2) the Staurotypinae, Carettochelyidae, and Trionychidae share a common ancestor not shared by the Kinosterninae and Dermatemyidae (fig. 24C); and (3) the Dermatemyidae is the sister group to all other families of the Trionychoida.

This arrangement is supported by 28 characters from the present study, 17 of which suggest monophyly of the Trionychidae plus Carettochelyidae (table 20). These characters can be integrated with those used by Gaffney (1984) and Hutchison and Bramble (1981) to support the arrangement shown in figure 24C as the most parsimonious for the Trionychoida.

Monophyly of the Kinosternidae, Carettochelyidae, and Trionychidae is suggested by two characters of the shell, one of the cervical series and one of the pelvis. In all members of these three families there are 20 or fewer peripherals (character 5) and plastral buttresses lack pleural contact (character 26). The ventral process of the eighth cervical is double (fig. 19) except in the trionychids in which this process is absent (character 86). In the pelvis, a thelial process (fig. 21) is present in kinosternids and Carettochelyids but is absent in nearly all trionychids (observed only in specimens of Lissemys, MHNG 615.87, UMMZ 129396, UF 56017) (character 103).

The inclusion of the Trionychidae and Carettochelyidae in the same clade as the Kinosternidae in the Hutchison and Bramble (1981) arrangement requires that these taxa share the features shown to be derived for the Dermatemyidae plus kinosternids in that study. However, scutes are absent from all trionychids and in carettochelyids only the vertebral scutes develop and these are lost soon after hatching (Zangerl, 1959); thus the many characters of sculation used by Hutchison and Bramble (1981) do not enter into the current argument. Many of the remaining characters of their dermatemyid-kinosternid clade are shared by the Trionychidae and Carettochelyidae: posterior lobe reduced in width, stapedial artery reduced, large costiform processes, reduction of plastral bridge. Two other characters which they use, megacephaly and the tricarinate carapace, are actually quite variable within the Dermatemyidae and Kinosternidae. Megacephaly is as well developed in some trionychids (Trionyx cartilagineus and especially T. subplanaus) as it is in megacephalous kinosternids (Claudius angustatus, Sternotherus minor). The tricarinate carapace is certainly absent in some dermatemyids and in some kinosternines. The reduction of carapacial keeling could very likely be a result of the flattening of the shell which occurs in the clade leading to trionychids.

The one remaining nonscute character which Hutchison and Bramble (1981) considered to be evidence of monophyly of the Kinosternidae plus Dermatemyidae, exclusive of the Trionychidae and Carettochelyidae, is the loss of sculpturing of the shell. There would have to be reversal in this character to allow the arrangement advocated here.

Two of the nonscute characters cited by Hutchison and Bramble (1981) for monophyly of the Kinosternidae are characters which I cite as evidence for the monophyly of the Kinosternidae, Trionychidae, and Carettochelyidae. These are the possession of 20 (or fewer) peripherals (character 5) and the presence of a double ventral process of the eighth cervical (character 86).

Other characters that these authors cite for the monophyly of the Kinosternidae do not necessarily exclude the Trionychidae and Carettochelyidae from this clade. These include: the loss of neural eight, the tendency for development of a secondary palate, and development of impressed musk ducts in the anterior peripherals.

Although most kinosternids have seven or fewer neurals, both Staurotypus species have eight (numbers two through nine) on occasion (UF 58976, BMNH 1871.1.7.5). Other than lacking an independent first neural or preneural this is identical to the proposed primitive number for trionychids.

The development of a secondary palate is not widespread enough among kinosternids to be a valid shared derived feature of this family. Hutchison and Bramble (1981) cited Gaffney (1979b) in support of this feature. Gaffney mentioned the presence of a secondary palate only in two genera (Staurotypus and xenochelys). The palate in the other genera of this family are not remarkably elongate. This character is of value at a lower level.
of universality (subfamily Staurotypinae) than it is assigned in the Hutchison and Bramble arrangement.

Impressed musk ducts are clearly visible on the interior surface of the anterior peripherals (usually numbers two, three, and four) of all kinosternids. In Carettochelys, there is no duct impression but there is a canal through the second peripheral. The interior opening of this canal is at the same level as the impressed duct in kinosternids, the exterior opening is identical in position to the anterior musk duct opening in trionychids. It is apparent that all trionychoids have anterior musk ducts which exit just dorsal to the forelimbs. In kinosternids they leave an impression in the anterior peripherals; in Carettochelys, there is no duct impression but there is a canal through the second peripheral. Trionychids have no anterior peripherals so the path of the musk duct cannot be traced in osteological material. The condition in Carettochelys could be viewed as a modification of that seen in the kinosternids.

From the osteological evidence it appears that the best arrangement for the Trionychoida is to regard the Dermatemydidae as a sister group to the other three families. Furthermore, it is apparent that certain kinosternids have closer affinities to the carettochelyids and trionychids than others.

Monophyly of the Staurotypinae, Carettochelyidae, and Trionychidae

One line of evidence pursued in the present study supports monophyly of the Staurotypinae, Carettochelyidae, and Trionychidae, and evidence from Hutchison and Bramble (1981) supports this view. The palate of all three living species of staurotypines develops a foramen intermaxillaris (character 47). It does not appear until maturity but it forms in exactly the same manner as in carettochelyids and trionychids. It lies between the vomer and premaxillae with maxillae defining the lateral edges. In staurotypines it allows the symphyseal hook of the lower jaw to pass into the nasal capsule. In other cryptodires with well-developed symphyseal hooks, this region of the palate is usually deeply impressed (Chelydra, Macroclemys, Platysternon) or the premaxillae may be slightly divided (Depreochelys) but in no other turtles is there an opening comparable to the foramen intermaxillaris.

All four of the nonscute features used by Hutchison and Bramble (1981) for evidence of monophyly of the Staurotypinae are shared by the Trionychidae and Carettochelyidae. These are: (1) costal bone four spans peripheral six (carettochelyids); (2) the anterior lobe is kinetic; (3) there are very short plastral buttresses; and (4) scapular attachment is transferred from entoplastron to epiplastron. I find the second feature to be useful at a higher level and I have used it as evidence for monophyly of the Kinosternidae, Carettochelyidae, and Trionychidae. Attachment of the scapulae to the epiplastron via the acromial ligament has been verified for Carettochelys and the Trionychidae (Bramble and Carr, MS). This feature may occur in kinosternines only because the entoplastron is absent and thus it may not be homologous to the condition in Staurotypines, Carettochelys, and trionychids.

The osteological data support an arrangement of the families of the Trionychoida that has not been considered previously. That is, monophyly of the Staurotypinae, Carettochelyidae, and Trionychidae (fig. 24C). That the entire Kinosternidae might be the sister group to the carettochelyid-trionychid clade (fig. 24B) is an alternative possibility.

Monophyly of the Kinosternidae exclusive of the Trionychidae and Carettochelyidae is suggested by four characters in addition to those treated by Hutchison and Bramble (1981). These are: (1) the presence of one dorsal and one lateral opening of the foramen nervi auriculotemporalis (character 97); (2) two, rather than one, posterior thoracic vertebrae having transverse processes that fail to reach the carapace (character 89); (3) the presence of an ilioischial notch (Zug, 1971; character 110); and (4) the presence of clapping or stridulating organs in most species. However, the most parsimonious arrangement of the osteological data results in the arrangement shown in figure 24C.

Monophyly of the Carettochelyidae and Trionychidae

Since it was first described, Carettochelys has often been associated with the Trionychidae (Baur, 1891b; Hummel, 1929;
TABLE 20
Shared Derived Characters of the Trionychidae and Carettochelyidae

<table>
<thead>
<tr>
<th>Character code</th>
<th>Character state</th>
</tr>
</thead>
<tbody>
<tr>
<td>6</td>
<td>peripherals never sutured to pleurals</td>
</tr>
<tr>
<td>28</td>
<td>rib heads strongly sutured to vertebral centra</td>
</tr>
<tr>
<td>30</td>
<td>shell is sculptured and without epidermal scutes</td>
</tr>
<tr>
<td>44</td>
<td>premaxillae fused</td>
</tr>
<tr>
<td>46</td>
<td>basisphenoid contacts palatines</td>
</tr>
<tr>
<td>50</td>
<td>vomer not in contact with pterygoids</td>
</tr>
<tr>
<td>56</td>
<td>foramen posterius canalis caroticus interni</td>
</tr>
<tr>
<td>94</td>
<td>50% or more of area articularis mandibularis</td>
</tr>
<tr>
<td>99</td>
<td>retroarticular process forms about one-tenth of jaw</td>
</tr>
<tr>
<td>83</td>
<td>cervical centra 2–7 opisthocoelous</td>
</tr>
<tr>
<td>52</td>
<td>processus pterygoideus not projecting</td>
</tr>
<tr>
<td>81</td>
<td>radius and ulna in contact adjacent to manus</td>
</tr>
<tr>
<td>82</td>
<td>number of clawed digits three or fewer</td>
</tr>
<tr>
<td>105</td>
<td>epipubic region never ossifies</td>
</tr>
<tr>
<td>113</td>
<td>coracoid longest of three pectoral processes</td>
</tr>
<tr>
<td>37</td>
<td>quadrate enclosing stapes</td>
</tr>
<tr>
<td>27</td>
<td>carapace not sutured to plastron</td>
</tr>
</tbody>
</table>

* States for characters 6 through 83 are unique among the Cryptodira. States for characters 52 through 113 are also found among the Chelonioida. The state for 37 is also found in the Testudinidae and Chelydridae. That for 27 is also found in both the Chelonioida and Chelydridae.

Monophyly of the family Trionychidae has, to my knowledge, never been questioned. All recent systematic studies treat the family as a monophyletic unit (De Broin, 1977; Gaffney, 1975, 1979b, 1984; Bickham and Carr, 1983; Meylan, 1985), but the osteological evidence for monophyly has never been compiled. Therefore, the unique features of the family are listed in table 21. In combination these synapomorphic features result in the unique overall morphology of this distinctive family of turtles.

### TABLE 21
Uniquely Derived Features of the Trionychidae

<table>
<thead>
<tr>
<th>Character code</th>
<th>Character state</th>
</tr>
</thead>
<tbody>
<tr>
<td>5</td>
<td>18 or fewer peripherals; no pygal or suprapygal</td>
</tr>
<tr>
<td>22</td>
<td>boomerang-shaped entoplastron</td>
</tr>
<tr>
<td>33</td>
<td>quadrate jugal not in contact with postorbital</td>
</tr>
<tr>
<td>35</td>
<td>jugal contacts parietal</td>
</tr>
<tr>
<td>45</td>
<td>premaxillae excluded from aperture narium externum</td>
</tr>
<tr>
<td>80</td>
<td>hyperphalangy of manus digits 4 and 5, pes digit 4</td>
</tr>
<tr>
<td>82</td>
<td>three clawed digits in manus</td>
</tr>
<tr>
<td>84</td>
<td>centra of eighth cervical and first body vertebra not in contact</td>
</tr>
<tr>
<td>85</td>
<td>no ventral processes on eighth cervical</td>
</tr>
<tr>
<td>90</td>
<td>corpus hyoideum composed of six or eight ossifications</td>
</tr>
<tr>
<td>101</td>
<td>ilia curve posteriorly</td>
</tr>
<tr>
<td>106</td>
<td>pectinal processes in a single plane and in broad contact with plastron</td>
</tr>
<tr>
<td>108</td>
<td>pectinal processes equal to or wider than interpubic contact</td>
</tr>
</tbody>
</table>

Ramsay, 1886; Siebenrock, 1909; Walther, 1922). It is clear from the characters considered in the current study that this association is very well supported by osteological data (table 20). Ten of the features shared by these two families occur in no other cryptodire. Five others are present in these two families and among the Chelonioida. The state for 37 is also found in the Testudinidae and Chelydridae; that for 27 is also found in both the Chelonioida and Chelydridae.

### RELATIONSHIPS AMONG THE RECENT TRIONYCHIDAE

Computer-assisted analyses of independent data sets from the skull, shell, and non-shell postcrania reveal that there are numerous possibilities for explaining the character state distributions of each data set by using hypotheses of descent that require a mini-
imum number of evolutionary steps. By recognizing unresolvable areas in the multiple, equal-length arrangements suggested by each data set, a single solution or consensus tree for that data set was obtained. These fundamental cladograms vary between data sets in the degree of resolution of interfamilial relationships, in their internal consistency (the amount of parallelism and reversal required by the distribution of the character states), and most importantly, in their topology. The relationships suggested by analysis of the skull data (fig. 26) differ from those obtained by analysis of shell data (fig. 25). The poor resolution achieved by the small nonshell postcranial data set (fig. 27) limits the comparability of the topology resulting from its analysis to that resulting from analysis of shell or skull characters.

Results of analyses of the three separate data sets (i.e., the fundamental cladograms, figs. 25–27) could not be resolved into a single general cladogram following the methods of Adams (1972) or Nelson (1979). Therefore, these results are contrasted and compared to one another and to six equally parsimonious trees (figs. 29, 30) based on an analysis of all three data sets combined. This comparison suggests a choice of two alternative trees as the best hypotheses for the relationships of soft-shelled turtles from osteological evidence (figs. 33, 34).

Evidence from Shell Morphology

A previous examination (Meylan, 1985) has indicated that there is sufficient variation in shell morphology among the shells of trionychids to allow resolution of the relationships of 20 of the 22 living species. The arrangement which resulted from that study is based on 16 characters and the most parsimonious tree was produced by hand (fig. 28). That data set has been upgraded for the current study. The present shell data matrix includes 40 percent more entries (21 characters × 22 taxa vs. 16 characters × 20 taxa). With this increase in data a search for the most parsimonious tree proved to be too time consuming by hand. A tree-producing package was used to determine the most parsimonious arrangement of the Trionychidae based on shell data. This analysis produced a dozen equally parsimonious trees. This is due entirely to alternative topologies of the unresolvable portions of the trees. Two clades that appear in all of the shortest-length trees cannot be fully resolved by analysis of the data from the shell alone. These problematical clades are a group of Cyclanorbines (Cycloderma aubryi, Cycloderma frenatum, and Lissemys punctata) and the Indian species of the genus Trionyx. These two clades are shown to be unresolved in the tree which best represents the relationships of the Trionychidae based on shell morphology alone (fig. 25).

These results are generally compatible with those of Meylan (1985). The monophyly of the Trionychinae is supported. Monophyly of the Indian species and its position as the sister group to the remaining Trionychinae is also repeated. The Asian species occupy the middle ground between the Indian clade and a previously recognized clade leading to the North American forms.

The most obvious divergences from the previous arrangement (Meylan, 1985) are the failure to recognize a monophyletic Cyclanorbinae and the recognition of most Asian species as a monophyletic group. In this regard these results support the conclusions of De Broin (1977) who suggested that the Cyclanorbinae may not be monophyletic and that the Trionychinae includes three monophyletic groups, the Indian forms (her Aspiderites), most other Asian forms (her Amyda), and a group which culminates in the North American forms (her Platypeltis).

The failure of analysis of the current shell data to support a monophyletic Cyclanorbinae, contrary to the findings in Meylan (1985), can be attributed to the inclusion of several new characters not considered in that study. Cyclanorbis elegans shares with the Trionychinae a reduction in length of the bony bridge and articulation of the ilia against the cartilaginous part of the shell rather than on the bony disc (characters 21 and 23). These characters work in concert with reduced plastral callosities, a short nuchal bone, and the united anterior and posterior costiform processes (characters 1, 2, and 9) to suggest that the two Cyclanorbis species share a unique common ancestor with the Trionychinae. However, the distribution of two characters which support monophyly of the Cyclanor-
Fig. 25. The most parsimonious cladogram of extant soft-shelled turtles based on 22 characters of shell morphology. The characters defining each node are as follows: Node 1: - 1(2) nuchal more than two times wider than long, - 5(4) peripherals absent, - 10(2) hyo- and hypoplastra fuse just after hatching, - 13(2) posterior process of hypoplastra lateral to anterior process of xiphiplastra, - 14(2) eight or nine neurals (after reversal to primitive condition at node 9, occurs again in steindachneri), - 16(2) pleurals seven and eight or eight only meet on midline (after reversal at node 8, occurs again in steindachneri), - 17(2) "boomerang-shaped" entoplastron. Node 2: - 19(2) epiplastra I-shaped, - 25(2) carapacial margin straight or concave posteriorly. Node 3: - 1(3) nuchal bone three or more times wider than long, - 2(2) anterior and posterior costiform processes united, - 3(2) anterior edge of first body vertebra located at middle of nuchal (occurs also in aubryi). Node 4: - 9(3) four or fewer plastral callosities (reverses twice), - 21(2) no depressions for the ilia on the eighth pleurals, - 22(2) bridge short. Node 5: - 10(1) hyo- and hypoplastra do not fuse just after hatching (a reversal), - 13(1) anterior process of xiphiplastra lateral to posterior process of hypoplastra (a reversal), - 17(3) point of neural reversal at neural six or seven or anterior. Node 6: - 9(2) five callosities present in plastron (a reversal that occurs also in cartilagineus), - 20(2) anterior projection of epiplastron of intermediate length. Node 7: - 4(2) first and second neurals fused. Node 8: - 16(1) only eighth pleurals meet on midline (a reversal). Node 9: - 14(1) nine neurals (fused one and two count two; a reversal). Node 10: - 17(2) point of neural reversal at neural seven (a reversal). Node 11: - 20(3) anterior process of epiplastron long. Node 12: - 24(2) largest adult size 200 mm or less (occurs also at node 17). Node 13: - 14(3) eight or fewer neurals (fused first and second count as two). Node 14: - 8(2) eighth pleurals reduced in size. Node 15: - 9(4) two plastral callosities (occurs also in elegans). Node 16: - 15(3) position of neural reversal highly variable, - 17(5) point of posteriormost neural reversal at neural four, five, or six, - 29(2) sexual dimorphism in disc size (occurs also in indica). Node 17: - 9(1) up to seven callosities present in plastron (a reversal). Node 18: - 1(4) nuchal four or more times wider than long (occurs also in subplanus), - 14(2) eight or nine neurals present (a reversal; fused one and two count two). Species characters: punctata: - 5(3) 14 to 18 peripherals present, - 7(2) prenuchal bone present (occurs also in senegalensis), - 14(4) seven or eight neurals present. aubryi: - 3(2) anterior edge of first body vertebra located at middle of nuchal (occurs also in puncticata). - 17(1) neural reversal occurs at neural eight (a reversal which occurs also in elegans). senegalensis: - 7(2) prenuchal bone present (occurs also in punctata), - 9(0) nine or more callosities in the plastron, - 14(5) seven or fewer neurals, - 16(4) additional pleurals to six, seven and eight meet at midline. elegans: - 1(2) nuchal two times wider than long (a reversal that also occurs in formosus.
Fig. 25 (continued), and steindachneri. — 9(4) two plastral callosities (occurs also at node 15), — 17(1) neural reversal occurs at neural eight (a reversal that occurs also in aubryi). indica: — 3(3) anterior edge of first body vertebra occurs at anterior edge of nuchal, — 29(2) sexual dimorphism in disc length (occurs also at node 16), formosus: — 1(2) nuchal two times wider than long (a reversal that occurs also in elegans and steindachneri). cartilagineus: — 9(2) five callosities in plastron (a reversal that occurs also at node 6), steindachneri: — 1(2) nuchal two times wider than long (a reversal that occurs also in elegans and formosus), — 14(2) eight or nine neurals (fused one and two count two), — 16(2) pleurals seven and eight or eight only meet at midline (a rederived feature after reversal to the primitive condition at node 8). subplanus: — 1(4) nuchal four times wider than long (occurs also at node 18), — 15(2) point of neural reversal is always at adjacent neurals (also in hurum and gangeticus), — 16(0) no pleurals meet on midline. sinensis: — 8(1) eighth pleurals not reduced in size (a reversal), — 20(3) anterior process of epiplastra long, — 29(1) no sexual dimorphism (a reversal).

Evidence from Skull Morphology

Like variation in the trionychid shell, variation in the trionychid skull is sufficient to allow nearly complete resolution of the relationships of all 22 living species.

Analysis of 23 characters of the trionychid skull using PAUP results in a minimum-length tree of 99 evolutionary steps. Three equally parsimonious trees produced by PAUP differ only in minor changes in the positions of Trionyx formosus and T. leithii. Variation in the three trees is represented in the single solution cladogram by a trichotomy (fig. 26). The three equally parsimonious cladograms otherwise agree completely in the remainder of their structure.

The three arrangements all support a monophyletic Cyclanorbinae as the sister group to a monophyletic Trionychinae. Liss- emys punctata is always the sister group to all other cyclanorbines. Chitra indica and Pelochelys bibroni form a clade which is the sister group to the remaining Trionychinae. Trionyx cartilagineus is the sister group to two remaining major monophyletic units, the North American group plus T. triunguis, T. euphraticus, and T. swinhoei on the one hand, and the Indian and Asian Trionyx species on the other. Unlike the arrangement based on shell morphology, T. sinensis is placed among the Asian clade and T. subplanus is placed among the Indian forms.

Although the arrangement based on skull data alone is initially more appealing for several reasons, its internal consistency is lower than that derived from shell data. The distribution of nearly two-thirds of the character states in the skull cladogram must be explained by reversal or parallelism. The appealing features of the skull arrangement include its support of both subfamilies, the Cyclanorbinae and Trionychinae, as monophyletic units and its overall similarity to the arrangement in Meylan (1985) which in turn approaches arrangements proposed by Love- ridge and Williams (1957) and De Broin (1977).
Fig. 26. The distribution of character states in the most parsimonious arrangement of extant soft-shelled turtles based on 23 characters of skull morphology. Evidence for the numbered nodes is as follows: Node 1: - 33(2) quadratojugal never contacts postorbital, - 34(2) jugal contacts parietal on skull surface in one-half of sample (occurs independently in subplanus and muticus after reversal at node 8), - 35(2) jugal always contacts parietal within temporal fossa, - 45(2) premaxillae always excluded from apertura narium externum, - 48(2) vomer never divides maxillae, - 53(2) foramen palatinum posterius small, - 60(2) foramen posterius canalis carotici interni within lateral crest of basioccipital tubercle, - 68(2) epipterygoid, when present, contacts palatine in one-half of sample. Node 2: - 54(2) foramen palatinum posterior forms in palatine only (occurs also in sinensis and swinhoei), - 58(2) foramen jugulare posteros, - 60(3) foramen palatum posterior canal carotic interni below lateral crest of basioccipital tubercle (occurs also at node 9). Node 3: - 34(3) jugal always contacts parietal on skull surface (also occurs at node 8 and in formosus), - 36(2) vomer does not contact prefrontal (occurs also in indica, reverses in elegans), - 47(2) vomer never reaches intermaxillary foramen (occurs also at node 8), - 64(2) basisphenoid sometimes medially constricted (occurs also at node 20 after reversal at node 16). Node 4: - 9(2) dorsal edge of apertura narium extemum weakly emarginate laterally (occurs also at node 8). Node 5: - 76(2) quadratojugal participates in processus trochlearis oticum (occurs also at node 8). Node 6: - 70(0) when epipterygoid is present pterygoid contacts foramen nervi trigemini between epipterygoid and quadrate or not at all, - 71(2) epipterygoid contacts prootic anterior to foramen nervi trigemini in one-half of sample (reverses at node 9), - 73(2) epipterygoid fuses to pterygoid only in adults (occurs also at node 5). Node 7: - 34(3) jugal always contacts parietal on skull surface (occurs also at node 3 and in formosus), - 48(1) vomer divides maxillae (a reversal), - 68(3) epipterygoid never contacts palatine (occurs also in senegalensis and frenatum). Node 8: - 76(2) quadratojugal participates in processus trochlearis oticum (occurs also at node 5 and in formosus), - 34(1) jugal never contacts parietal on skull surface (a unique reversal), - 41(2) dorsal edge of apertura narium externum weakly laterally emarginate (occurs also at node 4), - 49(2) vomer never reaches intermaxillary foramen (occurs also at node 3), - 64(2) basisphenoid sometimes medially constricted (occurs also at node 20 after reversal at node 16). Node 9: - 60(3) foramen palatinum posterior canal carotic interni below lateral crest of basioccipital tubercle (occurs also at node 9). Node 10: - 9(1) dorsal edge of apertura narium externum weakly emarginate laterally (occurs also at node 8). Node 11: - 76(1) quadratojugal never participates in proces-
sus trochlearis oticum (a unique reversal), —32(2) jugal contacts squamosal in one-half of sample (occurs also in muticus and swinhoei), —73(3) epipterygoid never fuses to pterygoid (occurs also at node 18, in cartilagineus and in indica). Node 12: —34(2) jugal contacts parietal on skull roof in one-half of sample (occurs also at node 1, in subplanus and in muticus). Node 13: —41(3) dorsal edge of aperture narium externum strongly laterally emarginate (occurs also at node 15), —59(2) foramen jugularis posterius excluded from fenestra postotica by descending process of opisthotic which reaches pterygoid (occurs also in subplanus, absent in hurum). Node 14: —31(1) quadrate jugal contacts maxillary (a unique reversal), —71(2) epipterygoid contacts prootic anterior to foramen nervi trigemini in 50% of sample (occurs also in cartilagineus, bibroni, and indica). Node 15: —41(3) dorsal edge of aperture narium externum strongly laterally emarginate (occurs also at node 13). Node 16: —78(2) parietal makes up 22.1% or more of the processus trochlearis oticum (occurs also in nigricans and elegans), —64(1) basiphenoid not medially constricted in ventral view (a unique reversal). Node 17: —48(2) vomer usually divides maxillae (a unique reversal), —74(2) intermaxillary foramen extends across 60 percent of primary palate. Node 18: —49(1) vomer reaches intermaxillary foramen (a reversal that occurs also in senegalensis), —73(3) epipterygoid never fuses to pterygoid (occurs also at node 11 and in cartilagineus and indica). Node 19: —48(1) vomer always divides maxillae (a reversal that occurs also at node 7 and in senegalensis). Node 20: —64(2) basiphenoid constricted in some individuals (occurs also in cartilagineus and subplanus). Species characters. aubryi: —53(4) foramen palatinum posterior forms in palatine only when epipterygoid is present (occurs also at node 1, in muticus, and indica), —65(2) premaxilla absent in some individuals. senegalensis: —48(1) vomer always divides maxillae (occurs also at nodes 7 and 19), —49(1) vomer reaches intermaxillary foramen (occurs also at node 18), —68(3) epipterygoid, when present, never contacts palatine (occurs also at node 7, in senegalensis and nigricans). elegans: —36(1) vomer contacts prefrontals (a unique reversal), —68(1) epipterygoid, if present, always contacts the palatine (occurs also at node 9). frenatum: —53(4) foramen palatinum posterior is divided into many small openings (occurs also in frenatum, —65(2) premaxilla absent in some individuals. senegalensis: —48(1) vomer always divides maxillae (occurs also at nodes 7 and 19), —49(1) vomer reaches intermaxillary foramen (occurs also at node 18), —68(3) epipterygoid, when present, never contacts palatine (occurs also at node 7, in nigricans and senegalensis). indica: —36(2) vomer never contacts prefrontal (occurs also at node 3), —65(3) premaxilla usually absent, —71(3) epipterygoid always contacts prootic anterior to foramen nervi trigemini (occurs also in steindachneri), —73(3) epipterygoid never fuses to pterygoid (occurs also at nodes 11 and 18 and in cartilagineus), —74(0) intermaxillary foramen less than 7 percent of primary palate length, —75(0) postorbital bar twice length of orbit. cartilagineus: —73(3) epipterygoid never fuses to pterygoid (occurs also at nodes 11 and 18 and in indica). hurum: —59(1) foramen jugulare posterior is not excluded from fenestra postotica (a reversal). steindachneri: —34(3) jugal always contacts parietal on skull surface (occurs also at nodes 3 and 7 and in formosus), —71(3) epipterygoid always contacts prootic anterior to foramen nervi trigemini (occurs also in indica), —75(2) postorbital bar very narrow, less than one-fifth orbit width (occurs also in muticus, spiniferus, and subplanus). sinensis: —54(2) foramen palatinum posterior forms in palate only (occurs at node 2 and in swinhoei), —70(2) when epipterygoid is present pterygoid contacts foramen nervi trigemini between epipterygoid and parietal or not at all —76(2) quadrate jugal participates in processus trochlearis oticum (occurs also at nodes 5 and 9). formosus: —34(3) jugal always contacts parietal on skull surface (occurs at nodes 3 and 7 and in steindachneri). leitiili: —70(0) when epipterygoid is present, pterygoid contacts foramen nervi trigemini between epipterygoid and quadrate or not at all (occurs also at node 6). nigricans: —60(2) foramen postorius canalis carotic interni located in lateral crest of basioccipital tubercle (occurs also in bibroni, cartilagineus, and indica), —68(3) epipterygoid, when present, never contacts palatine (occurs also at node 7 and in senegalensis), —78(2) parietal makes up 22.1% or more of processus trochlearis oticum (occurs also at node 16 and in elegans). subplanus: —34(2) jugal contacts parietal on skull surface in one-half of sample (occurs also at node 12, in punctata and in muticus), —59(2) foramen jugulare posterius excluded from fenestra postotica by descending process of opisthotic (occurs also at node 13), —75(2) postorbital bar less than one-fifth of orbit width (occurs also in spiniferus, muticus, and sinensis), muticus: —32(2) jugal contacts squamosal in one-half of sample (occurs also at node 11 and in swinhoei), —34(2) jugal contacts parietal on skull surface in one-half of sample (occurs also at node 12, in punctata and subplanus), —69(2) contact between pterygoid and foramen nervi trigemini never occurs when epipterygoid is present (occurs also at node 3 and in steindachneri), —75(2) postorbital bar less than one-fifth of orbit width (occurs also in spiniferus, sinensis, and subplanus. swinhoei: —32(2) jugal contacts squamosal in one-half of sample (occurs also at node 11 and in muticus), —41(2) dorsal edge of aperture narium externum weakly laterally emarginate (a reversal that occurs elsewhere only in euphraticus), —54(2) foramen palatinum posterior forms in palate only (occurs also at nodes 3 and 7 in muticus and subplanus), —70(2) when epipterygoid is present, pterygoid contacts foramen nervi trigemini between epipterygoid and parietal or not at all (occurs also in sinensis). euphraticus: —41(2) dorsal edge of aperture narium externum weakly laterally emarginate, a reversal that occurs elsewhere only in swinhoei).
Fig. 27. The most parsimonious cladogram for extant soft-shelled turtles based on 13 characters of the mandible and nonshell postcrania. Evidence for each node is as follows: Node 1: — 79(3) entepicondylar foramen never closed (occurs also in the Staurotypinae and in Cheloniidae), — 80(2) hyperphalangy of manus digits 4 and 5, pes digit 4 (absent only in senegalensis), — 82(2) three digits clawed, — 84(2) centrum of eighth cervical not in contact with centrum of first body vertebra, — 85(2) no ventral process of eighth cervical, — 90(2) six or more ossifications in corpus hyoideum, — 96(2) foramen nervi auriculotemporalis usually with two lateral openings (occurs also in emydids and some pleurodires), — 101(2) ilia curve posteriorly, — 102(2) ilia are not expanded distally (occurs also in all Kinosternidae), — 106(2) pectoral processes and interpubic suture lie in a single plane (occurs also in Claudius), — 108(2) pectoral processes equal to or wider than interpubic contact. Node 2: — 93(2) basihyals in close contact and projecting anteriorly, — 98(2) foramen intermandibularis caudalis never enclosed by prearticular (occurs also in indica, formosus, and swinhoei), — 109(2) metischial processes very weakly developed (occurs also at node 12). Node 3: — 107(1) ischia extend slightly into thyroid fenestra (reversal of feature shared by Staurotypinae, Carettochelyidae, and Trionychidae). Node 4: — 88(2) strong dorsal processes present on posterior cervicals. Node 5: — 112(2) angle of acromion process to scapula approaches that of coracoid to acromion (occurs also at nodes 9 and 10). Node 6: — 91(2) two or more ossifications in second branchial horn, — 113(2) coracoid longest of three pectoral processes (occurs also in punctata). Node 7: — 95(2) a strong ridge present in a depression on the symphysis. Node 8: — 87(2) a distinct ventral keel present on the posterior end of the eighth cervical (occurs also at node 13), — 90(3) eight ossifications in corpus hyoideum (occurs also at node 11 and in gangeticus). Node 9: — 88(2) strong dorsal processes on posterior cervicals (occurs also at node 4), — 92(2) ossifications of second branchial horn very broad and strongly sutured, — 95(1) no ridge on symphysis (a unique reversal), — 112(2) angle of acromion process to scapula approaches that of coracoid to acromion (occurs also at nodes 5 and 10). Node 10: — 112(2) angle of acromion process to scapula approaches that of coracoid to acromion (occurs also at nodes 5 and 9). Node 11: — 90(3) eight ossifications in corpus hyoideum (occurs also at node 8 and in gangeticus). Node 12: — 91(3) seven or more ossifications in second branchial horn (occurs also in gangeticus and spiniferus), — 109(2) metischial processes not well developed (occurs also at node 2). Node 13: — 87(2) distinct ventral keel on posterior end of eighth cervical (occurs also at node 8). Specific characters. punctatus: — 113(2) coracoid longest of three pectoral processes (occurs also at node 6). indica: — 98(2) foramen intermandibularis caudalis never enclosed by prearticular (occurs also at node 2 and in formosus and swinhoei). hurum: — 91(1) only one ossification in second branchial horn (a unique reversal). gangeticus: — 90(3) eight ossifications
in corpus hyoidis (occurs also at node 8 and node 11), – 91(3) seven or more ossifications in the second branchial horn (occurs also at node 12 and in spiniferus). formosus: – 98(2) foramen intermandibularis caudalis never enclosed by prearticular (occurs also at node 2 and in indica and swinhoei), spiniferus: – 91(3) seven or more ossifications in second branchial horn (occurs also at node 12 and in gangeticus). swinhoei: – 98(2) foramen intermandibularis caudalis never enclosed by prearticular (occurs also at node 2 and in indica and formosus).

**EVIDENCE FROM NONSHELL POSTCRANIA AND LOWER JAW**

Only 13 characters of the lower jaw and nonshell postcrania were found to display useful interspecific variation among living trionychids. This is far too few to allow complete resolution of the relationships of the Recent Trionychidae. Two pairs of species share identical character state distributions (Cycloderma aubryi and Cycloderma frenatum; Trionyx nigricans and T. leithii) and three other species share another distribution (T. steindachneri, T. sinensis, and T. triunguis). Furthermore, two additional species, T. swinhoei and T. formosus, have numerous missing values. The lack of resolvability and the presence of many missing values result in hundreds of equally parsimonious trees. But even among the numerous trees are some consistently repeated nodes.

Examination of a large subset (N = 45) of these trees reveals that nine clades appear in every one. These provide important evidence for intrafamilial relationships and are shown in a consensus tree (fig. 27). Most importantly, the Cyclanorbinae and Trionychinae are recognized in every case. The former has a unique configuration of the corpus hyoidis (character 93), lacks distinct metischial processes (character 109), and never has the foramen intermandibularis caudalis defined by bone (character 98). The latter has multiple ossifications of the second branchial horn (character 91) and the coracoid is longer than the scapula (character 113) in every case (and also in Lissemys punctata).

A unique reversal to the primitive condition of ischial projections into the thyroid fenestra (character 107) and reduction of the acromion process to scapula angle (character 112), each identify a separate clade within the Cyclanorbinae.

Among the Trionychinae, one large subset of taxa, the four Indian species plus *Trionyx formosus, T. cartilagineus, Chitra indica*, and *Pelechelys bibroni* are recognized as a single clade largely on the basis of a symphysal ridge (character 95). Four characters of the nonshell postcrania support monophyly of *Chitra* and *Pelechelys*.

The remaining trionychine species always include three additional clades. *Trionyx muticus* and *T. spiniferus* share a rare configuration of the scapula (character 112). *T. subplanus, T. euphraticus, T. swinhoei*, and *T. ferox* have eight ossifications of the corpus hyoidis (character 90), also found in *T. cartilagineus, Chitra, and Pelechelys*. *T. euphraticus* and *T. ferox* have a high number of ossifications in the second branchial horn (character 91) and lack distinct metischial processes (character 109).

Although variation in the characters of the lower jaw and nonshell postcrania are insufficient to allow formulation of an independent arrangement of the Recent trionychids, certain of these characters are important in corroborating clades identified by the shell and skull data sets. Also, some characters which have proven unimportant at this level are essential to formulation of a hypothesis for the higher relationships of the Trionychidae.

**FORMULATION OF A GENERAL HYPOTHESIS OF RELATIONSHIPS FOR THE TRIONYCHIDAE**

The methods available for constructing consensus trees (Adams, 1972 and Nelson, 1979) will not completely resolve the relationships among Recent soft-shelled turtles. The Adams (1972) method combines information from nodes present in every rival tree. There is only one node, that representing the Trionychinae, found in all three fundamental cladograms. The Nelson (1979) method combines replicated nodes as the foundation for a consensus tree; uncombinable nodes are discarded and combinable nodes, which are unreplicated but compatible with one another, are added to the replicated nodes. Only six
nodes are replicated in two or more of the fundamental cladograms in this study and four combinations of combinable unreplicated nodes can be added to produce a consensus tree which contains an equal amount of cladistic information (an equal number of nodes).

As an alternative, I have made a clade-by-clade comparison of the trees resulting from analysis of the shell data (fig. 25) to that resulting from the data on the skull (fig. 26) and the mandible and nonshell postcrania (fig. 27). These results are then compared to those based on a separate PAUP analysis of all three data sets combined (figs. 33, 34).

All three cladograms based on independent data sets and those from the combined data set consist of basal cyclanorbines, and a series of similar combinations of Indian, Asian, and North American species. It is simplest to compare and combine results by proceeding up the cladogram.

**Cyclanorbinae:** Monophyly of the Cyclanorbinae has been advocated by several students of trionychid systematics (Boulenger, 1889; Deraniyagala, 1939; Loveridge and Williams, 1957; Meylan, 1985). It is supported strongly by the skull and nonshell data sets (figs. 26, 27) but does not appear in the arrangement based on the shell alone (fig. 25). As pointed out in Meylan (1985) the unique cyclanorbine xiphiplastral-hypoplastral joint and early fusion of the hyo- and hypoplastra (characters 10, 13) can be considered shared derived characters for the subfamily rather than unique reversals for the Trionychinae as shown in figure 25. These two characters, in combination with the unique cyclanorbine hyoid (character 93) restriction of the fenestra postotica by an ascending pterygoid arch (character 58), the absence of distinct metistial processes (character 109), and other characters of the skeleton and soft parts (including femoral flaps) suggest that recognition of a monophyletic Cyclanorbinae would ultimately lead to a more parsimonious arrangement of the Trionychidae. If the shell arrangement (fig. 25) is used, the distribution of seven nonshell characters common to these five taxa would require 21 evolutionary steps. On the other hand addition of the shell data to the skull arrangement would require only seven added steps, provided that the genus Cyclanorbis (elegans plus senegalensis) is considered to be monophyletic. Monophyly of the Cyclanorbinae is indicated in all six equally parsimonious trees based on the combined data set.

Resolution of the Cyclanorbinae is best completed by recognizing three monophyletic genera, *Lissemys* (*L. punctata*), *Cyclanorbis*, and *Cycloderma* (aubryi plus frenatum), with *Lissemys* being the sister group to the other genera. This arrangement requires that two steps be added to account for independent acquisition of epiplastron shape and shell shape (characters 19 and 25) in *Lissemys* and *Cycloderma*. But the retention of the shell topology would require independent acquisition of seven characters in *Cycloderma* and *Cyclanorbis* and would add seven evolutionary steps. Among the characters supporting monophyly of *Cyclanorbis* plus *Cycloderma* are the reduced size of the coracoid (character 113), medial curvature of the ilia (lost in *Cyclanorbis elegans*; character 109), the presence of a small and multiply divided foramen palatinum posterius (character 53), and exclusion of the quadrate from the trigeminal foramen by the epipterygoid (character 71). Three of the four species also lack prefrontal-vomer contact, an absence found elsewhere only in *Chitra indica* (character 36).

Monophyly of *Cyclanorbis* is suggested by ischial extension into the thyroid fenestra (character 107), reduced angle of the acromion process to body of scapula (character 112), wide nuchal (character 1), united costiform processes (character 2), and the location of the first thoracic vertebra in the middle of the nuchal bone (character 3). *Cycloderma* has a unique condition of the foramen palatinum posterius: it is represented by many very fine openings hardly distinguishable from the nutritive foramina of the palate (character 53). The two species of the genus also share characters of shell shape and epiplastron shape (characters 19, 25), which are found also in *Lissemys*, and the presence of enlarged dorsal processes on the cervical series which occur elsewhere only in *Chitra indica* and *Pelochelys bibroni* (character 88).

The six equally parsimonious cladograms for the combined data set match three arrangements of the Cyclanorbinae (fig. 29) to two arrangements of the Trionychinae (fig.
One of the alternative cyclanorbin arrangements is that advocated above (fig. 29B). The other two require either a paraphyletic Cyclanorbis or a paraphyletic Cycloderma.

Choice between these equally parsimonious arrangements for the Cyclanorbinae rests on further considerations of the characters. Variability in the number of pleurals that meet on the midline (character 16) provides useful data that enhance the argument for recognition of a monophyletic Cyclanorbis. The modal condition of the neural series was used to score taxa in table 3. However, the highly derived condition (state 4 of character 16), common in Cyclanorbis senegalensis, is also known to occur in Cyclanorbis elegans (see section on neurals under variation in shell morphology). Using Cartmill's (1978) philosophy, that occasionally derived is in fact derived, the rare occurrence of a high number of pleurals meeting at the midline in Cyclanorbis elegans reinforces the suggestion of monophyly for this genus which appears in two of the three alternative topologies for the Cyclanorbinae (fig. 29).

Recognition of a monophyletic Cyclanorbis reduces the choice of topologies for the Cyclanorbinae to those shown in figure 29B and C. Examination of the characters which support monophyly of Cycloderma (fig. 29B) versus those which support monophyly of Cycloderma aubryi plus Cyclanorbis (fig. 29C) provides useful results relevant to determining the relative reliability of these two alternative arrangements. The two characters which argue for monophyly of Cycloderma include one unique evolutionary event, the reduction of the foramen palatinum posterius to a series of fine openings (character 53), and a feature which occurs elsewhere on only one occasion, the presence of large dorsal spines on the cervical vertebrae (fig. 20, character 88). The average consistency of these characters is 0.750. The average consistency of the three characters which support monophyly of Cycloderma aubryi and Cyclanorbis (fig. 29C) is much less, 0.431. These include anterior location of the first thoracic vertebra (character 3, C = 0.667), location of neural reversal (character 17, C = 0.375), and emargination of the prefrontals in the apertura narium externum (character 41, C = 0.250). On the strength of its higher consistency at the critical level (see Wheeler, 1986), it is suggested that the arrangement of the Cyclanorbinae that appears in figure 29B is the most reliable hypothesis.
Fig. 29. The three alternative topologies for the subfamily Cyclanorbinae, each of which appears in two of six equally parsimonious cladograms of the Trionychidae based on combined skull, shell, and nonshell postcranial evidence. Based on details of character 16 and higher internal consistency of critical characters, alternative B is used in the solution cladogram.

nonshell arrangements (figs. 26, 27) support a monophyletic Trionychinae. In all, nine characters support the recognition of this subfamily (figs. 33, 34). Unique features of the Trionychinae include advancement of the point of reversal of neural orientation at least to neural six or seven and the presence of multiple ossifications of the second branchial horn (characters 17 and 91). Four other features of the Trionychinae appear independently in one or both Cyclanorbis species (characters 1, 2, 21, and 23).

The basic difference between the arrangement of the Trionychinae determined from shell versus skull data is the combination of the Asian and North American clades to the exclusion of the Indian clade in the shell arrangement and the combination of the Indian, North American, and parts of the Asian clades to the exclusion of Chitra, Pelochelys, and Trionyx cartilagineus in the skull arrangement. These differences are based on very few characters. More importantly, the four major clades which appear in the analyses of all three data sets combined always appear in either the skull or shell arrangement or both. At this point it seems best to consider the evidence for recognition of these four major clades within the Trionychinae. Consideration of a hypothesis about their interrelationship can then follow.

Four groups of species within the Trionychinae are represented as distinct clades or are in close proximity in at least two of the three arrangements based on the three independent data sets and in all most parsimonious arrangements based on united data sets. These are termed the North American clade, the Indian clade, the Trionyx cartilagineus clade, and the T. steindachneri clade.

The North American clade includes three Old World species, Trionyx triunguis, T. euphraticus, and T. swinhoei, as well as the three North American forms, T. ferox, T. muticus, and T. spiniferus. This clade also includes T. sinensis in the arrangement based on shell data. All members of this group have eight or fewer neurals (character 14), deeply emarginate prefrontals (character 41), and a large contribution by the parietal to the processus trochlearis oticum (character 78). Except for T. triunguis, the members of this clade also have a large foramen intermaxillaris (character 74), second branchial horns which ossify from seven or more centers (character 91), and small to absent eighth pleurals (character 8).

The Indian clade includes Trionyx gangeticus, T. leithii, T. hurum, and T. nigricans.
The evidence that this group should be recognized comes entirely from the shell. All our species have a maximum of five plastral allosities, epiplastral extensions of intermediate length, and two neurals between the first pair of pleurals (characters 4, 9, and 20). The presence of two neurals between the first pair of pleurals may be primitive for the Trionychinae but in that case an extra neural must have been added to the anterior end of the neural series in the common ancestor of II trionychids. Only one appears between the first pleurals in carettochelyids, kinosternids, and dermatemydids. The addition of neural one in the ancestral trionychid and the subsequent fusion of neurals one and two called in Meylan (1985) are two independent vents. However, the appearance of two neurals between the first pleurals could alternatively be explained by independent vents in the Cyclanorbinae and in the Indian forms of Trionyx. In the various arrangements under consideration here T. formosus and some of the members of the T. steindachneri group may be included in the Indian clade.

The Trionyx steindachneri group appears to include T. sinensis and T. subplanus. Although these three taxa are not combined in any of the three cladograms based on the three separate data sets, they form a monophyletic group in all six of the equally parsimonious cladograms resulting from analysis of all data combined (figs. 30, 33, 34). The most important character of this group is the unique division of the fenestra postotica by a descending process of the opisthotic in T. sinensis, T. steindachneri, and T. subplanus. Furthermore, in T. sinensis the pterygoid contacts the foramen nervi trigemini anterior to the epipterygoid, unlike the condition in the members of the North American clade in which the contact is posterior to the epipterygoid (see discussion of character 70). T. sinensis also lacks the high number of ossifications in the cornu branchiale II, the significant contribution of the parietal to the processus trochlearis oticum, the large foramen intermaxillaris, and the secondarily enlarged vomer found in all members of the North American clade (characters 91, 78, 74, 48, and 49). Recognition of a clade consisting of T. sinensis, T. steindachneri, and T. subplanus requires that the highly variable neural formula with the last reversal in neural orientation occurring at neural six (characters 15 and 17) and the reappearance of callosities on all plastral elements (character 9) occur independently in T. sinensis and in the North American clade. However, reversal of reduction in the eighth peripheral and of sexual size dimorphism which are required in the shell arrangement are not required if T. sinensis is withdrawn from the North American clade.

The last of the four groups of species within the Trionychinae includes Trionyx cartilagineus, Chitra indica, and Pelochelys bibroni. These three species have the foramen posterior canalis caroticus interni lying within, rather than below, the lateral crest of the tuberculum basioccipitale, a condition seen elsewhere only in the single available skull of T. nigricans (character 60). The epipterygoid frequently contacts the prootic anterior to the foramen nervi trigemini (character 70), and...
the eighth cervical vertebra has a distinct ventral ridge (character 87) in all three. Furthermore, these taxa all have a hyoid with eight elements in the corpus hyoidis which occurs elsewhere only in T. subplanus and in three species of the North American clade. The highly derived nature of Chitra and Pelochelys is suggested by their many shared derived features and the unique features of Chitra.

The shell characters that conflict with the nonshell evidence for monophyly of these three taxa are relatively minor. An extra posterior neural may appear at times in Chitra indica and Trionyx cartilagineus and neural reversal may occur one neural more posteriorly in some cases (characters 14 and 17). The clearest conflict in character distribution is the presence of elongate anterior epiplastral projections (character 20) in T. cartilagineus and in the Indian and T. steindachneri groups. Recognition of these groups requires that elongate epiplastra arise independently on three occasions.

The resolution of the species of the Trionychinae into four clades seems clear and it results in the recognition of groups which other authors have recognized and even named in the past. To finish the task of determining the best hypothesis for relationships among all members of this subfamily, it is necessary to identify the interrelationships of these four clades. Unfortunately, there are few characters which contribute to the understanding of the relationship of these clades to one another and several alternative hypotheses are possible.

Based on the presence of a symphyseal ridge (character 95) (which is absent in species with a short symphysis or reduced overall size) and a constricted basisphenoid (character 64), all of the Indian and Asian forms could be the sister group of the North American clade (fig. 31). Within this Indian and Asian clade, the Trionyx cartilagineus group stands out as being highly derived. A sister group to the T. cartilagineus group could be defined on two features of the skull: contact of the jugal and squamosal across the quadratojugal (character 32) and contact of jugal and parietal on the skull surface (character 34). These characters occur in some individuals of nearly every species in the Indian clade and in T. sinensis. Only the latter character is present in T. steindachneri and T. subplanus, but the distribution of other characters suggests that the absence of the former is best considered as a reversal.

This arrangement (fig. 31) is the most parsimonious one that will preserve the four species groups as monophyletic units. It is four steps longer than the two shortest trees based on analysis of the skull, shell, mandible, and nonshell postcrania combined.

The two alternative arrangements of the Trionychinae based on the analysis of the combined data sets differ only in the placement of the four trionychine clades (figs. 30, 33, 34). In both, the Indian species group is paraphyletic and the only difference is that the North American forms are the sister group to the Trionyx cartilagineus group on the one hand, and to the T. steindachneri group on the other. No supplementary evidence is available to support one of these arrangements over the other. Consequently, until additional data can be collected and analyzed, the arrangements shown in figures 33 and 34 must be considered equally plausible, most parsimonious hypotheses for the interfamilial relationships of the Trionychidae. The revised classification which follows reflects the uncertainties which remain in our understanding of trionychid relationships (fig. 32).

**Comparison of Results to the Prevailing Hypotheses of Trionychid Relationships**

Although there is extensive literature on the taxonomy of soft-shelled turtles, few authors have considered the systematic relationships of all of the family members. The few exceptions are Hummel (1929), Loveridge and Williams (1957), and De Bröin (1977). Of these, the Loveridge and Williams treatment gives the most complete consideration of interfamilial relationships.

These three major systematic studies all recognize at least three of the five species groups thought to represent monophyletic (or paraphyletic) clades in the current study. The Cyclanorbinae and the Indian and North American groups retain their identity in all three. The uniqueness of the genera Pelochelys...
lys and Chitra is recognized in each, as is the possible relationship of Trionyx sinensis to T. steindachneri.

Since the time of Boulenger (1889) and Lydekker (1889), soft-shelled turtles that hide their hind feet with flaps of skin have been recognized to be unique relative to other soft-shelled turtles. Only De Broin (1977) questioned the monophyletic nature of this subfamily. The 12 shared, derived features of this subfamily (figs. 33, 34) strongly support its continued recognition. Furthermore, the nine derived features of the Trionychinae indicate monophyly for the remaining trionychids which have previously been placed together without attention to their unique common ancestry.

Loveridge and Williams (1957) detailed the relationships of the African members of the Cyclanorbinae in terms of a progression of what they considered to be the most primitive form, Cyclanorbis elegans, to the most derived form, Cycloderma aubryi, based on three skull characters. The arrangement of the Cyclanorbinae given in their figure 50 (reproduced here as a cladogram in fig. 1) is identical to one of three alternatives for the Cyclanorbinae derived here (fig. 29A) but not chosen as the best solution. However, they supported monophyly of Cyclanorbis and Cycloderma, as is suggested by the data considered in the current study.

The Indian clade is recognized in all three previous systematic studies of the family. It has been based in part on the presence of a preneural although this may be primitive for the family. Hay (1904) proposed the name Aspideretes for those fossil and Recent trionychine species with a preneural. Hummel (1929) endorsed the use of this term as a subgenus, and De Broin (1977) recognized it alternatively as a valid genus or subgenus. In spite of its apparent paraphyletic nature, recognition of this distinctive taxon may best promote a more complete understanding of trionychine relationships.

De Broin (1977) and Loveridge and Williams (1957) found Trionyx formosus and T. cartilagineus to be closely related to the Indian clade. The results of this study suggest that T. formosus is the sister group of the four Indian species (but that it does not share the features of Aspideretes). T. cartilagineus is thought to share a unique common ancestor with Chitra and Pelochelys.

In past studies the North American clade
Fig. 32. A cladogram of trionychid relationships derived from the classification supported by this study. The use of a single branch point for the four tribes within the Trionychinae reflects uncertainty about the interrelationships of these four monophyletic groups.

is as frequently recognized as the Indian clade. The present analyses suggest that it includes *Trionyx triunguis*, *T. euphraticus*, *T. swinhoei*, and the three living North American species, *T. muticus*, *T. spiniferus*, and *T. ferox*. No previous study has included *T. triunguis* in this group. Loveridge and Williams (1957) placed *T. triunguis* in a sister group to the North American clade along with *T. sinensis* and *T. steindachneri* (fig. 1). These three species are united only because they each fail to share features of the distinctive groups which these authors recognized. De Broin (1977) considered *T. triunguis* as the remnant of a group that evolved independently from that which led to the North American forms. Based on the osteological features considered here, *T. triunguis* is best considered the sister group of the remainder of the North American clade. The remainder of this clade is recognized in the three previous systematic works and the name *Platypeltis* Fitzinger 1835 was applied to it by Hummel (1929). De Broin (1977) would restrict the use of the name *Platypeltis* to the three North American forms and resurrect the name *Rafetus* Gray 1864 for *T. swinhoei* and *T. euphraticus*. Although *Rafetus* Gray could be applied to these two Old World members of this clade, *Apalone* Rafinesque 1832 (*Trionyx spiniferus* LeSeuer 1827 type species) has priority over *Platypeltis* Fitzinger 1835 and would have to be applied to the three North American forms.

Fortunately, the systematic position of *Trionyx triunguis* is clear. It can stand alone in the arrangement of the family as described above. This is important taxonomically because it is the type species of *Trionyx*. The long muzzle of this species makes it phenetically distinct and the separation of the exoccipital from the pterygoid by the basisphenoid (character 63) is unique and makes it cladistically recognizable.

In past considerations of trionychid relationships the species *Trionyx sinensis* and *T. steindachneri* appear to have been left over after other more distinctive taxa had been
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extracted from the Trionychinae. Loveridge and Williams (1957) mentioned the unique feature shared by these two taxa (and also *T. subplanus*), division of the fenestra postotica by a ventral process of the opisthotic, but they do not make full use of this unique quality. In addition to this skull character, these two species and *T. subplanus* share characters of reduced total size and an extremely short nuchal bone. Smith and Smith (1980) indicated that the generic name *Amyda* Geoffroy has *Trionyx cartilagineus* as its type species and thus cannot be applied to this clade as has been suggested by De Broin (1977) and Hummel (1929). The first available name is *Pelodiscus* Gray 1844 for which *T. sinensis* is the type species.

The last of the four trionychine clades recognized in the current study includes *Pelochelys*, *Chitra*, and *Trionyx cartilagineus*. More than 100 years ago Gray (1873a) recognized a unique relationship between *Chitra* and *Pelochelys* by making them the only members of their subfamily Chitrina of the family Chitridae. Although no authors have followed this arrangement, none have disputed it.

The sister group relationship of *Trionyx cartilagineus* to *Chitra* and *Pelochelys* proposed here is novel. But based on a unique location of the foramen posterior canalis carotic interni (character 60), frequent contact of the epipterygoid and prootic anterior to the foramen nervi trigemini (character 71), absence of contact of epipterygoid and palatine (character 68), and the presence of a fine ridge on the centrum of the eighth cervical vertebra (character 87), the sister relationship of *T. cartilagineus* to these unique genera is well supported. Recognition of the *T. cartilagineus* clade as a single genus seems undesirable given the established quality of the names *Pelochelys* and *Chitra*. But *T. cartilagineus* deserves distinction from the rest of the genus *Trionyx*. In this case the generic name *Amyda* Geoffroy, for which *Testudo cartilaginea* Boddart (1770) is the type species, should be applied to *T. cartilagineus* (Smith and Smith, 1980).

In summary, the clades recognized by phylogenetic analysis are in nearly every case not totally novel. All have had generic or subgeneric names applied to them. The unique qualities of these clades are not currently conveyed by the broad use of the name *Trionyx* but could be by the use of the available generic names as in the classification which follows (summarized in table 22). If more com-

### Table 22

**Summary of Classification of the Trionychidae Suggested by This Study**

<table>
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<tr>
<th>subclass</th>
<th>family</th>
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<th>species</th>
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<td><em>C. elegans</em> (Gray, 1869)</td>
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<td><em>Cycloderma</em> Peters, 1854</td>
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<td><em>C. aubryi</em> (A. Dumeril, 1856)</td>
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<td><em>C. frenatum</em> Peters, 1854</td>
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<td>Lissemydini</td>
<td><em>Lissemys</em> Malcom Smith, 1931</td>
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<td><em>A. mutica</em> (Le Sueur, 1827)</td>
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<td><em>P. steindachneri</em> (Siebenrock, 1906)</td>
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complete resolution of the interrelationships of the four identified trionychine clades can be achieved, further increase in information content of trionychid classification could result from the use of supertribes to contain tribes of unique common ancestry.

TRENDS AND MECHANISMS IN SOFT-SHELLED TURTLE EVOLUTION

Although it is possible to trace the changes in character states during the course of evolution of trionychids, many possibilities exist that might explain why these changes have occurred. Three adaptive scenarios could explain portions of the unique morphology of trionychids: (1) selection for greater snapping ability (Pritchard, 1984); (2) selection for high-speed swimming (Pritchard, 1984; personal obs.); and (3) selection for greater aquatic fossoriality (Pritchard, 1984; Bramble, personal commun.).

The apparently critical evolutionary step which allows the unique loss of peripherals in trionychids occurs in carettochelyids. This is the very tight and broad suturing of the rib heads to the vertebral centra. The development of massive rib heads provides a structural alternative to the use of the plastron (via the peripherals) as a tension member (Richmond 1964; Bramble, personal commun.). The peripherals are not strongly sutured to the pleurals in Carettochelys and it is unlikely that the plastron is as effective a tension member in this genus as it is in turtles with solid pleuroperipheral and bridge contacts.

The absence of peripherals can most easily be explained by developmental truncation. In the embryonic turtle, ossification centers in the disc margin (those which result in the peripherals, nuchal, and pygal bones) are the last to form (Zangerl, 1969). Consequently, the trionychid shell may be paedomorphic; that is, the final step in carapace development never occurs.

Paedomorphosis may be the mechanism by which the unique trionychid shell morphology evolved. However, few other features of soft-shelled turtles can be ascribed to a truncation of development. The only characters which might also be a result of paedomorphosis are those of the pubic elements. As noted, the pectineal processes of the pubic bones lie in a single plane as appears to be the case early in ontogeny of other turtles. Furthermore, ossification of the prepubic region, which occurs in most living cryptodires, never occurs in trionychids. The absence of other paedomorphic features of soft-shelled turtle morphology suggests that developmental truncation has not been an overriding influence on the evolution of the group.

The most completely described adaptive hypothesis for the unique shell form of trionychids is that of Pritchard (1984). He suggested that Chitra is the best model for the ancestral trionychid, and that the unique body form of trionychids is an adaptation for a rapid predatory strike (one of his three listed adaptations for piscivory). His evidence is partly based on the similarity of the skull of Chitra to that of Chitracephalus dumonii Dollo 1884 from the Jurassic or Cretaceous of Europe, and partly on his observation that Chitra is the most developed piscivore among the trionychids and that other forms have secondarily become more generalized.

Other than their similar skull shape, there is nothing to suggest that Chitracephalus is related to the trionychids (Gaffney, 1979b). Pritchard himself stated that the long, narrow skull found in these two forms appears a number of times in turtle evolution. He cites Glyptops (a pleurosternid) and Deirochelys (an emydid) as examples. The superficial similarity of Chitracephalus and Chitra goes beyond the overall skull shape: both have large and well-developed hyoids. However, judging from unpublished stereo photographs of the type of Chitracephalus, the corpus hyoidis in the type is not composed of multiple ossifications and what appears to be a jugalquadratojugal bar is actually the lower jaw. Thus, Chitracephalus has continuous cheek and temporal emargination which is not known elsewhere among the Cryptodira.

Further arguments against using Chitra as the ancestral trionychid can be taken directly from the phylogenetic analyses conducted in this study. The many unique features of Chitra (and Chitra plus Pelochelys) would have to be lost secondarily in all other trionychids. A good example is the extensive postorbital bar. The hypothesis supported by the phylogenetically analyzed data suggests that a very
narrow postorbital bar first allowed contact of the jugal and parietal and that expansion of this contact is secondarily increased in *Chitra* and other species in the family with long, narrow skulls. Other features, including extensive hyperphalangy (Boulenger, 1889), the presence of large dorsal spines on the fifth and sixth cervicals, the narrow symphysis, the very short nuchal bone with the first thoracic vertebra located at the anterior margin, and the unique hyoid with a massive corpus hyoidei of eight ossifications and large second branchial arch of three strongly sutured ossifications, would all have to appear and then be lost in the course of trionychid evolution. It is far more parsimonious to consider the genus *Chitra* as a highly specialized trionychid (with all of its derived features appearing only once). Conversely, Pritchard’s (1984) argument that *Lissemys punctata* is the most derived of trionychids remains unsupported. The view that it is the most primitive (Walther, 1922; Deraniyagala, 1939) is corroborated in the current study.

Pritchard (1984) suggested that swimming prowess and aquatic fossoriality are two secondary advantages of modification of shell shape in trionychids. Bramble (personal commun.) has also pointed out that fossorial activity is enhanced by the shape of the trionychid carapace. Certainly, the flattened body form of trionychids provides reduced resistance to motion through water, sand, or mud. It is only after the loss of peripherals in trionychids that there has been a remarkable decrease in the relative proportion of the total carapace made up by the bony disc. A concomitant increase in the flexible margin, which would assist in aquatic fossoriality, also occurs at this stage, indicating that fossoriality may in fact be a secondary result of peripheral loss, and not necessarily the cause for their loss.

Although trionychids have reduced shells, they are found living with turtle-eating crocodilians throughout much of their range. Their survival under such circumstances may be ascribed to crypsis or to their swimming speed. Trionychids may be among the fastest swimming freshwater turtles (see Webb, 1962, and references therein). It has been my observation that *Trionyx ferox* is the fastest swimming turtle that one encounters in clear Florida spring runs. Selection for better swimming ability could explain the acquisition of numerous derived features noted during the course of this study, especially those of the shell and girdles.

Trends toward reduction in shell size, including reduction in the number of peripherals, neurals, and plastral callosities, and reduction in the size of the eighth pleurals and the nuchal bone could all be attempts to tighten the shell, with shell streamlining as the result. Reduction of the bridge is important in allowing maximum retraction of the hind limbs for a maximum power stroke in swimming (Zug, 1971).

Loss of epidermal scutes may also act to reduce the weight of the shell. If Coldiron (1974) is correct in his hypothesis that dermal bone sculpturing acts to disperse stresses on broad areas of dermal bone (crocodilian and labyrinthodont skulls), sculpturing could be an alternative shell-strengthening mechanism to epidermal scutes in trionychids. Acquisition of hyperphalangy can be correlated with increased swimming prowess. Strong contact of the radius and ulna stiffens the forearm and probably produces a better paddle in trionychids, carettochelyids, and cheloniids. The reduction of the transverse processes of the tenth thoracic vertebra that occurs in all trionychoids might increase the capacity of the pelvic girdle to rotate and thus contribute to the very long hind-limb power stroke of trionychids (Zug, 1971). The expanded pectineal processes of the pelvic girdle and the relatively enlarged coracoids both provide additional surface area for muscle attachment. Thus it appears that selection for improved swimming speed would account for many of the derived features noted to occur in the Trionychidae.
Fig. 33. One of two most parsimonious arrangements of the living Trionychidae. Characters supporting the nodes are as follows: Node 1: The evidence for monophyly of the Trionychidae is summarized in table 21. Node 2: - 10(2) hyoplastra and hypoplastra fuse just after hatching, - 13(2) hyoplastra are lateral to xiphiplastra at hypo-xiphiplastral union, - 14(2) eight or nine neurals (reduced from always nine) (occurs also at node 19 and in indica and leithii), - 16(2) eighth pleural only or seventh and eighth pleurals meet on midline (occurs also at node 11), - 17(1) neural reversal always occurs at neural eight (may be primitive condition), - 34(2) jugal contacts parietal on skull surface in one-half of sample (occurs also at node 15 and in leithii and muticus), - 54(2) foramen palatinum posterius forms in palatine only (occurs also in sinensis and swinhoel), - 58(2) foramen jugulare posterior excluded from fenestra postotica by pterygoid arching to contact opisthotic, - 68(2) epipterygoid never contacts palatine when it is present (occurs also at nodes 10, 19, 25, 53, 68, 88, and 107), - 93(2) basihyals in close contact and projecting anteriorly, - 98(2) foramen intermandibularis caudalis never enclosed by prearticular (occurs also at node 12 and in indica and formosus), - 107(1) ischia extend into thyroid fenestra (reversal of a derived condition shared by most trionychids, carettochelyids, and staurotypine kinosternids), - 109(2) metischial processes not well developed (occurs also at node 11). Node 3: - 5(4) no peripheral elements (occurs also at node 6), - 34(3) jugal always contacts parietal on skull surface (occurs also at node 8 and in formosus and steindachneri), - 36(2) vomer not in contact with prefrontal (occurs also in indica and reverses in elegans), - 53(3) foramina palatinum posterius small and divided, - 69(2) no contact between pterygoid and foramen nervi trigemini when epipterygoid is present (occurs also in muticus and steindachneri), - 72(2) epipterygoid contacts prootic posterior to foramen nervi trigemini, - 100(2) ilia curve medially, - 113(1) coracoid shorter than either process of scapula (unique among trionychids). Node 4: - 19(2) epiplastra I-shaped (occurs also in punctata), - 25(2) carapace straight or concave posterolaterally (occurs also in punctata), - 53(4) posterior palatine foramen consists of many small foramina, - 68(3) epipterygoid never contacts palatine (occurs also at node 10, 19, 25, 53, 68, 88, and 107), - 88(2) strong dorsal processes on cervical (occurs also at node 9). Node 5: - 2(2) anterior and posterior costiform processes united (occurs also at node 6, 19, 25, 53, 68, 88, and 107), - 3(2) anterior edge of first body vertebra is in the middle of the nuchal bone (occurs also at node 6 and in aubryi), - 107(2) no extension of ischia into thyroid fenestra (occurs also at node 6), - 112(2) angle of acromion process to scapula approaches that of coracoid to acromion (occurs also at nodes 9 and 14). Node 6: - 1(3) nuchal at least three times wider than long (occurs also in senegalensis), - 2(2) anterior and posterior costiform processes united (occurs also at node 5), - 3(2) anterior edge of first body vertebra in the middle of the nuchal (occurs also at node 5), - 5(4) no peripheral bones (occurs also at node 3), - 9(3) four plastral
Fig. 33 (continued).
callotites (reversal to five occurs at node 16 and in cartilagineus), - 17(3) neural series reverses at neural six or seven or anterior to that point, - 21(2) depressions for ilia in eighth pleural absent (occurs also in elegans), - 23(2) bridge short (occurs also in elegans), - 41(2) dorsal edge of aperture narium externum weakly emarginate (occurs also in aubryi and senegalensis), - 64(2) basisphenoid occasionally medially constricted, - 73(3) epipterygoid never fuses to pterygoid, - 91(2) two or more ossifications in second branchial horn of hyoid, - 95(2) sphenoid medially constricted, - 68(1) epipterygoid always contacts palatine when present (a reversal that occurs also in elegans). Node 10: - 17(3) point of reversal of neural orientation at neural six or seven (occurs also at node 8), - 20(2) anterior extension of epiproct is intermediate. Node 11: - 16(2) pleurals seven and eight or eight only meet on midline (occurs also at node 2), - 34(1) jugal never contacts parietal on skull surface (a reversal that occurs also in cartilagineus). Node 12: - 15(2) neural reversal occurs at one of two adjacent neurals, - 32(1) jugal never contacts squamosal (a reversal), - 41(3) dorsal edge of aperture narium externum strongly laterally emarginate. Node 13: - 14(2) some individuals with only eight (rather than nine) neurals (fused one and two counted as two) (occurs also at node 2 and in bibroni and leithii), - 76(2) quadratojugal participates in processus trochoheiris ocicurn (occurs also in cartilagineus, elegans, and frenatum). Node 14: - 4(2) first and second neurals fused (occurs also at node 7), - 9(3) four callotities present in plastron (occurs also at node 8 and in formosus), - 95(1) symphyseal ridge absent (occurs also at node 8). Node 15: - 1(4) width of nuchal bone more than four times length (occurs also in muticus), - 20(3) anterior extension of epiproct is long (occurs also in cartilagineus), - 24(2) largest adult size 200 mm or less (occurs also at node 21), - 34(2) jugal contacts parietal on skull surface in one-half of sample (occurs also at node 2 and in hurum and muticus), - 59(2) foramen jugulare posteriorius excluded from fenestra postotica by descending process of opisthotic which reaches pterygoid, - 70(2) when epipterygoid is present, pterygoid contacts foramen nervi trigemini between epipterygoid and quadrate or not at all (occurs also at node 17 and in leithii), - 71(2) epipterygoid contacts prootic anterior to foramen nervi trigemini in about 50% of sample (occurs also in hurum), - 87(2) ventral keel on eighth cervical present and limited to posterior end of centrum (occurs also at node 19), - 90(3) eight ossifications make up corpus hyoidis (occurs also at node 18 and in hurum and subplana). Node 8: - 9(3) four callotities present in plastron (occurs also at node 14 and in formosus), - 17(3) reversal of neural orientation occurs at neural six or seven (occurs also at node 10), - 34(3) jugal always contacts parietal on skull surface (also occurs at node 3 and in formosus and steindachneri), - 41(1) dorsal edge of aperture narium externum not emarginate (a reversal that occurs elsewhere only in frenatum), - 48(1) vomer divides maxillae (a presumed reversal that occurs at neural 18 and in senegalensis), - 49(1) vomer reaches intermaxillary foramen (a presumed reversal that occurs also at node 18 and in punctata and senegalensis), - 64(1) basisphenoid not medially constricted (occurs also at node 17), - 68(3) epipterygoid never contacts palatine (occurs also at node 4 and in nigricans and senegalensis), - 88(2) strong dorsal processes present on cervicals five and six (occurs also at node 4), - 92(2) ossifications of second branchial horn broad and strongly sutured, - 95(1) no symphyseal ridge (occurs also at node 14), - 112(2) angle of acromion process to scapula approaches that of coracoid to acromion (occurs also at nodes 3 and 21). Node 9: - 32(2) jugal contacts squamosal in one-half of sample (occurs also in muticus, sinensis, and swinhoei), - 64(3) basisphenoid medially constricted, - 68(1) epipterygoid always contacts palatine when present (a reversal that occurs also in elegans).
Fig. 33 (continued).

eight ossifications in corpus hyoidis (occurs also at node 7), - 91(3) seven or more ossifications in second branchial horn (occurs also in gangeticus), - 109(2) metischial process not distinct (occurs also at node 2). Node 19: - 9(4) two callosities on plastron (occurs also in elegans), - 41(2) dorsal edge of apertura narium externum weakly laterally emarginate (a reversal that occurs also in gangeticus), - 87(2) weak ventral keel present on posterior end of eighth cervical (occurs also at node 7), - 98(2) foramen intermandibularis caudalis never enclosed by prearticular (occurs also at node 2 and in formosus and indica). Node 20: - 15(3) position of reversal of neural orientation highly variable, often two reversals present (occurs also in sinensis), - 17(4) point of reversal of neural orientation at neural six, - 29(2) sexual dimorphism in disc length. Node 21: - 9(1) seven callosities in plastron of large adults (a reversal that occurs also in sinensis), - 24(2) largest adult disc length 200 mm or less (occurs also at node 15), - 69(2) contact between pterygoid and foramen nervi trigemini is absent when epipterygoid is present (occurs also at nodes 3 and 16), - 75(2) postorbital bar less than one-fifth of orbit diameter (occurs also at node 16), - 90(2) six ossifications in corpus hyoidis (a reversal), - 109(1) metischial processes present and distinct (a reversal), - 112(2) angle of acromion process to scapula approaches that of coracoid to acromion (occurs also at nodes 3 and 8). Specific characters. aubryi: - 3(2) anterior edge of first body vertebra at middle of nuchal (occurs also at nodes 5 and 6), - 12(2) xiphiplastra may fuse on midline (occurs also in punctata), - 65(2) premaxillae occasionally absent (occurs also in punctata), - 68(2) epipterygoid, if present, fails to contact palatine in one-half of sample (a reversal), frenatum: - 3(1) anterior edge of first body vertebra lies at posterior edge of nuchal (a reversal that occurs also in punctata), - 17(2) reversal of neural orientation occurs at neural seven (occurs also at node 15), - 7(2) prenuchal bone present (occurs also at node 3), - 12(2) xiphiplastra fuse in large adults (occurs also in aubryi), - 14(4) seven or eight neurals, - 19(2) epiplastra l-shaped (occurs also at node 4), - 25(2) carapace straight or concave postero-laterally (occurs also at node 4), - 49(1) vomer reaches intermaxillary foramen (occurs also at nodes 8 and 18), - 65(2) premaxilla occasionally absent (occurs also in aubryi, frequently absent in indica), bibroni: - 14(2) eight or nine neurals (occurs also at nodes 2 and 13 and in leithii), - 73(2) epipterygoid fuses to pterygoid in adults only (occurs also in elegans, frenatum, gangeticus, muticus, subplanus, and triunguis), indic: - 3(3) anterior edge of first body vertebra at anterior edge of nuchal, - 29(2) sexual dimorphism in disc length, - 36(2) vomer does not contact prefrontals (occurs also at node 3), - 65(3) premaxillae usually absent, - 71(3) epipterygoid contacts prootic anterior to foramen nervi trigemini (occurs also in steindachneri), - 74(0) intermaxillary foramen about 7% of pinnary palate length, - 75(0) postorbital bar about two times orbit width, - 98(2) foramen intermandibularis caudalis never enclosed by prearticular (occurs also at nodes 2 and 19 and in formosus), cartilagineus: - 20(3) long anterior projections of epiplastra (occurs also at node 15), - 76(2) quadratjugal participates in processus trocholearis oticum (occurs also at node 13 and in elegans, frenatum, gangeticus, muticus, subplanus, and triunguis), - 76(2) quadratjugal participates in processus trocholearis oticum (occurs also at node 13 and in cartilagineus and frenatum), - 78(2) 22.1% or more of processus trocholearis oticum made up by parietal (occurs also at node 17 and in nigricans), senegalensis: - 1(3) nuchal more than three times wider than long (occurs also at node 6), - 7(2) prenuchal bone present (occurs also in punctata), - 9(0) nine callosities in plastron, - 14(5) seven or fewer neurals, - 16(4) pleurals in addition to numbers six, seven, and eight meet at midline, - 48(1) vomer divides maxillae (occurs also at nodes 8 and 18), - 49(1) vomer reaches intermaxillary foramen (occurs also at nodes 8 and 18 and in punctata), - 68(3) when present epipterygoid does not contact palatine (occurs also at nodes 4 and 8 and in nigricans). punctata: - 7(2) prenuchal bone present (occurs also at nodes 8 and 18 and in senegalensis), - 12(2) xiphiplastra fuse in large adults (occurs also in aubryi), - 14(4) seven or eight neurals, - 19(2) epiplastra l-shaped (occurs also at node 4), - 25(2) carapace straight or concave postero-laterally (occurs also at node 4), - 49(1) vomer reaches intermaxillary foramen (occurs also at nodes 8 and 18 and in senegalensis), - 65(2) premaxilla occasionally absent (occurs also in aubryi, frequently absent in indica), bibroni: - 14(2) eight or nine neurals (occurs also at nodes 2 and 13 and in leithii), - 73(2) epipterygoid fuses to pterygoid in adults only (occurs also in elegans, frenatum, gangeticus, muticus, subplanus, and triunguis), indic: - 3(3) anterior edge of first body vertebra at anterior edge of nuchal, - 29(2) sexual dimorphism in disc length, - 36(2) vomer does not contact prefrontals (occurs also at node 3), - 65(3) premaxillae usually absent, - 71(3) epipterygoid contacts prootic anterior to foramen nervi trigemini (occurs also in steindachneri), - 74(0) intermaxillary foramen about 7% of pinnary palate length, - 75(0) postorbital bar about two times orbit width, - 98(2) foramen intermandibularis caudalis never enclosed by prearticular (occurs also at nodes 2 and 19 and in formosus), cartilagineus: - 20(3) long anterior projections of epiplastra (occurs also at node 15), - 76(2) quadratjugal participates in processus trocholearis oticum (occurs also at node 13 and in elegans, frenatum, and steindachneri), formosus: - 1(2) nuchal between two and three times wider than long (a reversal that occurs elsewhere in steindachneri), - 9(3) four callosities in plastron (occurs also at nodes 8 and 14), - 34(3) jugal always contacts parietal on skull surface (occurs also at nodes 3 and 8 in steindachneri), - 98(2) foramen intermandibularis caudalis never enclosed by prearticular (occurs also at nodes 2 and 19 and in indica), leithii: - 14(2) eight or nine neurals (occurs also at nodes 2 and 13 and in bibroni and muticus), - 70(0) when epipterygoid is present, pterygoid contacts
Fig. 33 (continued).
foramen neri trigemini between epipterygoid and quadrate or not at all (occurs also at nodes 7 and 17). nigricans: — 60(2) foramen posterius canalis carotic interni occurs within lateral crest of basic-occipital tuberale (occurs also at node 7), — 68(3) when present epipterygoid does not contact palatine (occurs also at nodes 4 and 8 and in senegalensis), — 78(2) 22.1 % or more of processus trochlearis oticum made up by parietal (occurs also at node 17 and in elegans). hurum: — 34(2) jugal contacts parietal in one-half of sample (occurs also at nodes 2 and 15 and in muticus), — 71(2) epipterygoid contacts prootic anterior to foramen nervi trigemini in about one-half of sample (occurs also at node 7), — 90(3) eight ossifications in corpus hyoidis (occurs also at nodes 7 and 18 and in subplanus), — 91(3) seven or more ossifications in second branchial horn (a reversal that occurs also at node 19), — 73(2) epipterygoid fuses to pterygoid in adults only (occurs also in bibroni, elegans, frenatum, gangeticus, muticus, and triunguis), — 91(3) seven or more ossifications in second branchial horn (occurs also at node 2). sinensis: — 9(1) seven plastral callosities present in plastron (a reversal that occurs also at node 21), — 15(3) position of neural reversal highly variable with more than one reversal sometimes present (occurs also at node 20), — 17(4) posteroi sternum reversal present at neural six or anterior (occurs also at node 20), — 32(2) jugal contacts squamosal in one-half of sample (occurs also in formosus, leithii, nigricans, muticus, and swinhoei), — 54(2) foramen palatum postei rior forms in plastrine only (occurs also at node 2 and in swinhoei). steindachneri: — 1(2) nuchal between two and three times wider than long (a reversal that occurs elsewhere in formosus), — 15(1) position of neural reversal is always at the same neural (a reversal that occurs also at node 17), — 34(3) jugal always contacts parietal on skull surface (also occurs at nodes 3 and 8 and in formosus), — 71(3) epipterygoid always contacts prootic anterior to foramen nervi trigemini (occurs also in indica), — 76(1) quadrate jugal not participating in processus trochlearis oticum (a unique reversal). subplanus: — 14(1) nine neurals present (a unique reversal), — 16(0) no pleurals meeting at midline, — 64(2) basi sphenoid occasionally medially constricted (a unique reversal), — 73(2) epipterygoid fuses to pterygoid in adults only (occurs also in bibroni, elegans, frenatum, gangeticus, muticus, and triunguis), — 90(3) eight ossifications in corpus hyoidis (occurs also at nodes 7 and 18 and in hurum), — 95(2) symphysis ridge present and in a depression (occurs after loss at node 14). triunguis: 73(2) epipterygoid fuses to pterygoid in adults only (occurs also in bibroni, elegans, frenatum, gangeticus, muticus, and subplanus). euphraticus: — 46(1) basisphenoid fails to reach palatines (unique among trionychids), — 64(2) basi sphenoid occasionally medially constricted (a reappearance after loss at node 17). swinhoei: — 32(2) jugal contacts squamosal in one-half of sample (occurs also in formosus, leithii, nigricans, muticus, and sinensis), — 54(2) foramen palatinum postei rior forms in plastrine only (occurs also at node 2 and in sinensis). fer ox: — 11(2) hyoplastra and hypoplastra fuse in adults. spiniferus: — 64(2) basi sphenoid occasionally medially constricted. muticus: — 1(4) nuchal bone more than four times wider than long (occurs also at node 15), — 14(2) eight or nine neurals (occurs also at nodes 2 and 13 and in bibroni and leithii), — 32(2) jugal contacts squamosal in one-half of sample (occurs also in formosus, leithii, nigricans, muticus, and swinhoei), — 34(2) jugal contacts parietal on skull surface in one-half of sample (occurs also at node 2 and 15 and in hurum), — 49(2) vomer fails to reach intermaxillary foramen (a unique reversal), — 73(2) epipterygoid fuses to pterygoid in adults only (occurs also in bibroni, elegans, frenatum, gangeticus, subplanus, and triunguis), — 91(2) two or more ossifications in second branchial horn of hyoid.
Fig. 34. The second of two most parsimonious cladograms of the living Trionychidae. Characters supporting the nodes are as follows: Node 1: The evidence for monophyly of the Trionychidae is summarized in table 21. Node 2: - 10(2) hypoplastra and hypoplastra fuse just after hatching, - 13(2) hypoplastra are lateral to xiphiplastra at hypoxiphiplastral union, - 14(2) eight or nine neurals (reduced from always nine) (occurs also at node 19 and in indica and leithii), - 16(2) eighth pleurals only or seventh and eighth pleurals meet on midline (occurs also at nodes 10 and 17), - 17(1) neural reversal always occurs at neural eight (may be primitive condition), - 54(2) foramen palatinum posterius forms in palatine only (occurs also in sinensis and swinhoei), - 58(2) foramen jugulare posterior excluded from fenestra postotica by pterygoid arching to contact opisthotic, - 68(2) epipterygoid excluded from contact with palatine in 50 percent of cases where it is present (occurs also at node 8), - 93(2) basihyals in close contact and projecting anteriorly, - 98(2) foramen intermandibularis caudalis never enclosed by prearticular (occurs also at node 12 and in indica and formosus), - 107(1) ischia extend into thyroid fenestra (reversal of a derived condition shared by most trionychids, carettochelyids, and staurotypine kinosternids), - 109(2) metischial processes not well developed (occurs also at node 11). Node 3: - 5(4) no peripheral elements (occurs also at node 6), - 34(3) jugal always contacts parietal on skull surface (occurs also in formosus, indica, and steindachneri), - 36(2) vomer not in contact with prefrontal (occurs also in indica and reverses in elegans), - 53(3) foramina palatinum posterius small and divided, - 69(2) no contact between pterygoid and foramen nervi trigemini when epipterygoid is present (occurs also in muticus and steindachneri), - 72(2) epipterygoid contacts prootic posterior to foramen nervi trigemini, - 100(2) ilia curve medially, - 113(1) coracoid shorter than either process of scapula (unique among trionychids). Node 4: - 19(2) epiplastra I-shaped (occurs also in punctata), - 25(2) carapace straight or concave posterolaterally (occurs also in punctata), - 53(4) posterior palatine foramen consists of many small foramina, - 88(2) strong dorsal processes on cervicals (occurs also at node 9). Node 5: - 2(2) anterior and posterior costiform processes united (occurs also at node 6), - 3(2) anterior edge of first body vertebra is in the middle of the nuchal bone (occurs also at node...
Fig. 34 (continued).
6 and in *aubryi*, - 107(2) no extension of ischia into thyroid fenestra (occurs also at node 6), - 112(2) angle of acromion process to scapula approaches that of coracoid to acromion (occurs also at nodes 9 and 14). Node 6: - 13(1) nuchal at least three times wider than long (occurs also in *senegalis*), - 2(2) anterior and posterior costiform processes united (occurs also at node 5), - 3(2) anterior edge of first body vertebra in the middle process (occurs also in *frenatum*). Node 5: - 5(4) no peripheral bones (occurs also at node 3), - 9(3) four plastral callosities (reversal to 5 occurs at node 16 and in *cartilagineus*), - 17(3) orientation of neural series reverses at neural six or seven or anterior to that point, - 21(2) depressions for ilia in eighth pleural absent (occurs also in *elegans*), - 23(2) bridge short (occurs also in *elegans*), - 41(2) dorsal edge of apertura narium externum weakly emarginate (occurs also in *aubryi* and *senegalis*), - 73(3) epitypodygon never fuses to pterygoid, - 91(2) two or more ossifications in second branchial horn of hyoid, - 107(2) no extension of ischia into thyroid fenestra (occurs also at node 5). Node 7: - 4(2) first and second neurals fuse (occurs also at node 20), - 34(1) jugal never contacts parietal on skull surface (a reversal), - 70(0) when epitypodygon is present, pterygoid contacts foramen nervi trigemini between epitypodygon and quadrate or not at all, - 76(2) quadraotorugialg participates in processus trocholeus oticum (occurs also in *elegans*, *frenatum*, *gangeticus*, and *sinensis*), - 90(3) eight ossifications in corpus hyoideum. Node 8: - 60(2) foramen postorius canalis caroticum interni lies within ridges which extend laterally from the basioccipital tubercles (occurs also in *nigerican*, - 68(2) when present, epitypodygon fails to contact palatine in 50 percent or more of sample (occurs also at node 2 and in *nigerican*), - 71(2) epitypodygon contacts prootic anterior to foramen nervi trigemini in 50 percent or more of sample (occurs also in *harum* and *steindachneri*), - 87(2) a ventral keel present on posterior end of 8th cervical (occurs also in *euphraticus*). Node 9: - 34(3) jugal always contacts parietal on skull surface (also occurs at node 3 in *formosus* and *steindachneri*), - 41(1) no dorsal emargination of apertura narium externum (a unique reversal), - 48(1) vomer divides maxillae (occurs also at node 11 and in *senegalis*), - 49(1) vomer reaches intermaxillary foramen (occurs also at node 11, in *punctata* and in *senegalis*), - 68(3) when present, epitypodygon never contacts palatine (occurs also in *frenatum*, *nigerican*, and *senegalis*), - 76(1) no contribution by quadrotugal to processus trocholeus oticum (a reversal that occurs elsewhere in *steindachneri*), - 88(2) strong dorsal processes on cervical (occurs also at node 4), - 92(2) ossifications of second branchial horn broad and strongly sutured, - 112(2) angle of acromion process to scapula approaches that of coracoid to acromion. Node 10: - 14(3) eight or fewer neurals (fused one and two counted as two), - 16(2) seventh and eighth pleurals meet in some individuals (occurs also at node 2 and at node 17), - 41(3) dorsal edge of apertura narium externum strongly emarginate (occurs also at node 18), - 78(2) parietal makes up 22.1 percent or more of processus trocholeus oticum (occurs also in *elegans* and *nigerican*). Node 11: - 8(2) eighth pleurals reduced or absent, - 48(1) vomer divides maxillae (occurs also at node 9 and in *senegalis*), - 49(1) vomer reaches foramen intermaxillaris (occurs also at node 9, in *senegalis* and *punctata*), - 74(2) intermaxillary foramen about 60% of length of primary palate, - 91(3) seven or more ossifications in second branchial horn (also occurs in *gangeticus*), - 109(2) no distinct metischial processes (occurs also at node 2). Node 12: - 9(4) only two callosities on plastron (occurs also in *elegans*), - 41(2) dorsal edge of apertura narium externum weakly emarginate (a unique reversal to a condition widespread in the trionychinae), - 98(2) foramen interman- dibularis caudalis never enclosed by prearticular (occurs also at node 2, in *formosus* and *indica*). Node 13: - 15(3) location of neural reversals highly variable (occurs also in *sinensis*), - 17(4) posteriormost reversal occurs at neural six (occurs also in *sinensis*), - 29(2) sexual dimorphism in disc length (occurs also in *indica*). Node 14: - 9(1) seven plastral callosities (a reversal to most primitive condition which occurs also in *sinensis*), - 24(2) largest adult size about 200 mm or less disc length (occurs also at node 20), - 69(2) contact between pterygoid and foramen nervi trigemini does not occur when epitypodygon is present (occurs also at node 3 and in *steindachneri*), - 75(2) postortal bar very narrow, less than one-fifth orbit diameter (occurs also at node 21), - 90(2) six ossifications in corpus hyoideum (a reversal that occurs also in *triunguis*), - 109(1) metischial processes present and distinct (a unique reversal), - 112(2) angle of acromion process to scapula approaches that of coracoid to acromion (occurs also at nodes 5 and 9). Node 15: - 32(2) jugal contacts squamosal in about one-half of sample (occurs also in *euphraticus*, *muticus*, and *sinensis*), - 64(3) basi- sphenoïd almost always medially constricted, - 95(2) symphyseal ridge strong and in a depression (occurs also in *cartilagineus*). Node 16: - 9(2) five callosities present in plastron (a reversal that occurs also in *cartilagineus*), - 20(2) anterior processes of epiplastra of intermediate length. Node 17: - 16(2) seventh and eighth pleurals meet on midline in some individuals (occurs also at nodes
Fig. 34 (continued).

2 and 10). Node 18: — 15(2) neural reversal occurs at adjacent neurals, — 32(1) jugal never contacts squamosal (a unique reversal). Node 19: — 14(2) some individuals with eight neurals (fused first and second neurals counted as two, occurs also at node 2, and in bibroni), — 76(2) quadrate-jugal participates in processus trochlearis oticum (occurs also at node 7, and in elegans and frenatum). Node 20: — 1(4) nuchal bone four or more times wider than long (occurs also in muticus), — 4(2) first and second neurals fused (occurs also at node 7), — 20(3) anterior processes of epiplastra long (occurs also in cartilagineus), — 24(2) largest adult size about 200 mm disc length (occurs also at node 14), — 59(2) foramen jugulare posterius excluded from fenestra postotica by descending process of opisthotic which usually reaches pterygoid, — 70(2) when epiphyseal is present pterygoid contacts foramen nervi trigemini between epiphyseal and parietal or not at all. Node 21: — 9(3) four plastral callosities (a reversal to the common condition in trionychines), — 17(2) posteriormost neural reversal occurs at neural seven or anterior to it (a reversal that occurs also in cartilagineus and formosus), — 75(2) postorbital bar less than one-fifth of orbit diameter (occurs also at node 14). Specific characters. aubryi: — 3(2) anterior edge of first body vertebra at middle of nuchal bone (occurs also at nodes 5 and 6), — 12(2) xiphiplastra fuse in some individuals (occurs also in some punctata), — 41(2) dorsal edge of apertura narium externum weakly emarginate (occurs also at node 6 and in senegalensis), — 65(2) premaxillae usually absent. frenatum: — 68(3) epiphyseal, when present, never contacts palatine (occurs also at node 9, in nigricans and in senegalensis), — 73(2) epiphyseal fuses to pterygoid in adults only (occurs also in elegans, bibroni, triunguis, muticus, gangeticus, and subplanus), elegans: — 9(4) only two plastral callosities (occurs also at node 12), — 21(2) depressions on eighth pleurals for contact of ilia absent (occurs also at node 6), — 23(2) bridge short (occurs also at node 6), — 36(1) vomer contacts prefrontal (a unique reversal), — 42(2) dorsal edge of apertura narium externum mediately emarginate, — 68(1) when present, epiphyseal always contacts palatine (a unique reversal), — 73(2) epiphyseal fuses to pterygoid in adults only (occurs also in frenatum, bibroni, triunguis, muticus, gangeticus, and subplanus), — 100(1) ilia do not curve medially (a unique reversal). senegalensis: — 1(3) nuchal three times wider than long (occurs also at node 6), — 7(2) prenuchal bone present (occurs also in punctata), — 9(0) nine or more plastral callosities (includes gular pair), — 14(5) seven or fewer neurals, — 16(4) pleural bones, in addition to pairs six, seven, and eight, meet at the midline, — 41(2) dorsal edge of apertura narium externum weakly emarginate laterally (occurs also at node 6 and in aubryi), — 48(1) vomer divides maxillae (occurs also at nodes 9 and 11), — 49(1) vomer reaches intermaxillary foramen (occurs also at nodes 9 and 11 and in punctata), — 87(2) intermaxillary quite reduced, averaging 7% of primary palate, — 68(3) epiphyseal fuses to pterygoid in adults only (occurs also in frenatum, elegans, triunguis, muticus, gangeticus, and subplanus), indica: — 3(3) anterior edge of first body vertebra at anterior edge of nuchal bone, — 29(2) sexual dimorphism in disc length (occurs also at node 13), — 36(2) vomer fails to contact prefrontal (occurs also at node 3), — 65(3) premaxillae usually absent (occurs also in aubryi), — 71(3) epiphyseal always contacts prootic anterior to foramen nervi trigemini (occurs also in steindachneri), — 74(0) intermaxillary foramen quite reduced, averaging 7% of primary palate, — 75(0) postorbital bar about two times orbit diameter, — 98(2) foramen intermandibularis caudalis never enclosed by prearticular (occurs also at nodes 12 and in formosus). cartilagineus: — 9(2) five plastral callosities (a reversal that occurs also at node 18), — 17(2) posteriormost neural reversal occurs at neural seven (a character reversal that occurs also at node 21 and in formosus), — 20(3) anterior epiplastral process long (occurs also at node 20), — 64(2) basispHENoid occasionally mediately constricted (occurs also in euphraticus and spiniferus), — 95(2) strong symphyseal ridge present (occurs also at node 15). triunguis: — 73(2) epiphyseal fuses to pterygoid in adults only (occurs also in bibroni, frenatum, elegans, muticus, gangeticus, and subplanus), — 90(2) six ossifications in corpus hyoidis (a reversal that occurs also at node 14). euphraticus: — 64(2) basispHENoid occasionally mediately constricted (occurs also in cartilagineus and spiniferus), — 87(2) ventral keel present on posterior end of eighth cervical (occurs also at node 8). swinhoei: — 32(2) jugal contacts squamosal in one-half of sample (occurs also at node 15 and in muticus and sinensis), — 54(2) foramen palatinum posterior forms in palatine only (occurs also at node 2), ferox: — 11(2) hypo- and hypoplastra fuse in adults. spiniferus: — 64(2) basispHENoid me-
Fig. 34 (continued).

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1(4) nuchal bone four or more times wider than long (occurs also at node 20). — 32(2) jugal contacts squamosal in one-half of sample (occurs also at node 15 and in swinnoei and sinensis). — 34(2) jugal contacts parietal on skull surface in one-half of sample (unique occurrence after reversal at node 7). — 73(2) epiphragm fuses to pterygoid in adults only (occurs also in bibroni, frenatum, elegans, muticus, subplanus, and tringuis). — 91(2) between two and six ossifications in second branchial horn of hyoid (a unique reversal).

formosus: — 1(2) nuchal bone only two times wider than long (a reversal that occurs also in steindachneri). — 17(2) last reversal in neural orientation occurs at neural seven (a character reversal that occurs also at node 21 and in cartilagineus). — 34(3) jugal always contacts parietal on skull surface (also occurs at nodes 3 and 9 and in steindachneri). — 98(2) foramen intermandibularis caudalis never enclosed by prearticular (occurs also at nodes 12 and in indica). leithii: — 14(2) some individuals with eight neurals (occurs also at nodes 2 and 19 and in bibroni). — 70(0) when epiphragm is present epiphragm contacts foramen nervi trigemini between epiphragm and quadratojugal or not at all (occurs also at node 7). nigricans: — 34(1) jugal never contacts parietal on skull surface (a reversal that occurs at node 7 and in gangeticus). — 60(2) foramen posterius carinalis caroticus interni located within a lateral crest of the basioccipital tubercle (occurs also at node 8). — 68(3) epiphragm does not contact palatine (occurs also at node 9 and in frenatum and senegalensis). — 78(2) parietal makes up 22.1% or more of processus trochlearis oticum. hurum: — 41(3) dorsal edge of aperture narium externum strongly emarginate laterally (occurs also at nodes 10 and 20). — 71(2) epiphragm contacts prootic anterior to foramen nervi trigemini in one-half of sample. — 90(3) eight ossifications in corpus hyoidis (occurs also at node 7 and in subplanus). — 91(1) a single ossification in the second horn of hyoid (a unique reversal). gangeticus: — 34(1) jugal never contacts parietal on skull surface (a reversal that occurs at node 7 and in nigricans). — 73(2) epiphragm fuses to pterygoid in adults only (occurs also in bibroni, frenatum, elegans, muticus, subplanus, and triunguis). — 91(3) seven or more ossifications in second branchial horn of hyoid (occurs also at node 11). sinensis: — 9(1) seven callosities in plastron (a reversal that occurs also at node 14). — 15(3) high variability of point of posteriormost neural reversal (occurs also at node 13). — 17(4) posteriormost neural reversal occurs at or anterior to neural six (occurs also at node 13). — 32(2) jugal contacts squamosal in one-half of sample (occurs also at node 15 and in muticus and swinnoei). — 54(2) foramen palatinum posteriorius located in palatine only (occurs also at node 2). — 95(1) symphysial ridge absent (a reversal that occurs also in steindachneri). steindachneri: — 1(2) nuchal bone only two times wider than long (a reversal that occurs also in formosus). — 15(1) neural reversal always occurs at the same neural (a unique reversal). — 34(3) jugal always contacts parietal on skull surface (also occurs at nodes 3 and 9 and in formosus). — 71(3) epiphragm contacts prootic anterior to foramen nervi trigemini (occurs also in indica). — 76(1) quadratejugal excluded from processus trochlearis oticum (a reversal that occurs also at node 9). — 95(1) symphysial ridge absent (a reversal that occurs also in sinensis). subplanus: — 14(1) nine neurals present (a unique reversal). — 16(0) no pleurals meet on midline. — 64(2) basisphenoid medially constricted on occasion (occurs also in cartilagineus, euphraticus, and spiniferus). — 73(2) epiphragm fuses to pterygoid in adults only (occurs also in bibroni, frenatum, elegans, muticus, triunguis, and gangeticus). — 90(3) eight ossifications in corpus hyoidis (occurs also at node 7 and in hurum).
TRIONYCHIDAE
(FITZINGER, 1826; AS TRIONYCHOIDEA)
BELL, 1828

TYPE GENUS: Trionyx Geoffroy, 1809.
DIAGNOSIS: Members of the Trionychidea (sensu Gaffney, 1975, 1984) with 18 or fewer peripherals, no pygal or suprapygal, a boomerang-shaped entoplastron, quadratojugal not contacting postorbital, jugal contacting parietal, premaxillae fused and excluded from apertura narium externum by maxillae, hyperphalangy of manus digits four and five and pes digit four, three clawed digits in manus and pes, cervical centra all opisthocoelous except eighth which lacks central articulation to first thoracic vertebra, no ventral process of eighth cervical vertebra, no ventral process of cervical vertebra, corpus hyoïdis composed of six or eight ossifications, ilia curve posteriorly, pectineal processes lie in a single plane and are in broad contact with plastron, and pectineal processes equal to or wider than interpubic contact.

CONTENT: Twenty-two living species divided among two subfamilies (the Cyclanorbinae and Trionychinae) and about 220 named fossil species, some of which are, on occasion, placed in a third subfamily, the Plastomeninae.

SUBFAMILY CYCLANORBINAE
HUMMEL, 1929

TYPE GENUS: Cyclanorbis Gray, 1854.
DIAGNOSIS: Members of Cyclanorbinae having no peripheral elements, medially curving ilia, coracoid shorter than either process of scapula, jugal always in contact with parietal on dorsal surface of skull, vomer not in contact with prefrontal (except in Cyclanorbis elegans), foramen palatinum posterius small and divided, no contact between pterygoid and foramen nervi trigemini when epipterygoid is present, and epipterygoid-prootic contact posterior to foramen nervi trigemini.

CONTENT: The four living species of this tribe belong to two genera, Cyclanorbis and Cycloderma.

Cyclanorbis Gray, 1854

TYPE SPECIES: Cyclanorbis senegalensis (Dumeril and Bibron, 1835).
DIAGNOSIS: Cyclanorbine trionychids, with the anterior and posterior costiform processes united, no extension of ischia into thyroid fenestra, angle between acromion process and body of scapula approaching that of acromion to coracoid, and a variable tendency of pleurals to divide the neural series by meeting on the midline.

CONTENT: Two species, Cyclanorbis senegalensis and Cyclanorbis elegans.

Cyclanorbis senegalensis

(type) (Dumeril and Bibron, 1835)

DIAGNOSIS: A species of Cyclanorbis with a prenuchal bone present, nine or more plastral callosities, seven or fewer neural bones, pleural bones in addition to numbers six, seven, and eight meeting on the midline, vomer dividing maxillae and reaching intermaxillary foramen, and epipterygoid never contacting palatine.
Cyclanorbis elegans (Gray, 1869)

Diagnosis: A species of Cyclanorbis with only two plastral callosities, no depressions on the eighth pleurals for articulation of ilia, a short bridge, the vomer in contact with the prefrontals; when present, epipterygoid always in contact with palatine, and apertura narium externum medially emarginate.

Cycloderma Peters, 1854

Type Species: Cycloderma frenatum Peters, 1854.

Diagnosis: Members of Cyclanorbini in which the epiplastra are I-shaped rather than J-shaped, the margin of the carapace is concave posterolaterally, the middle cervicals (4, 5, and 6) possess well-developed dorsal processes, and the posterior palatine foramina consist of numerous very small openings barely distinguishable from the nutritive foramina of the palate.

Content: Two living species, Cycloderma frenatum and Cycloderma aubryi.

Cycloderma frenatum Peters, 1854

Diagnosis: Members of Cycloderma in which the epipterygoid, when present, never contacts the palatine and fuses to the pterygoid in large adults, and in which the vomer is absent.

This species differs further from its living congener in retaining primitive features including the total absence of midline suturing or fusion of the xiphiplastra and in always retaining the premaxillae.

Cycloderma aubryi (A. Dumeril, 1856)

Diagnosis: Members of Cycloderma in which the xiphiplastra suture and fuse on the midline in large adults, the dorsal edge of the apertura narium externum is weakly emarginate, and premaxillae are usually absent.

TRIBE LISSEMYDINI
(WILLIAMS, 1950; AS LISSEMYDINAE)

New Rank

Type Genus: Lissemys Malcolm Smith, 1931.

Diagnosis: Cyclanorbine trionychids with a prenuchal bone, I-shaped epiplastra, posterolaterally concave carapacial margin and in which the xiphiplastra suture and fuse on the midline in large adults and the vomer reaches the intermaxillary foramen dorsal to the maxillae. Members of this tribe differ further from all other known trionychids by the primitive retention of peripheral elements.

Content: One genus Lissemys here considered to include a single species Lissemys punctata.

Lissemys Malcolm Smith, 1931

Type Species: Lissemys punctata (Lacépède, 1788).

Diagnosis: As for the tribe Lissemynidae. Content: As for the tribe Lissemynidae.

Lissemys punctata (Lacépède, 1788)

Diagnosis: As for the tribe Lissemynidae.

Subfamily Trionychinae
(FITZINGER, 1826; AS TRIONYCHOIDEA)

Lydekker, 1889

Type Genus: Trionyx Geoffroy, 1809.

Diagnosis: Trionychid turtles with the nuchal bone at least three times wider than long, anterior and posterior costiform processes united, no peripheral bones, neural series always containing at least one reversal of neural orientation, depressions for articulation of ilia absent from eighth pleural, a short bridge, two or more ossifications in the second branchial horn (except in some hurum), dorsal edge of apertura narium externum slightly to strongly emarginate, and epipterygoid typically fusing to pterygoid in adults.

Content: This study suggests that the subfamily Trionychinae consists of four monophyletic species groups. However, the relationships between the four groups is not totally resolved. To reflect this lack of resolution the recognition of four tribes is recommended below. By failing to designate groups between the rank of subfamily and tribe, the uncertainty about the interrelationships of these tribes can be indicated. In the interest of maintaining as much nomenclatorial stability as possible, the use of four tribes at this level is thought to be preferable to the recognition of four genera. The four tribes constituting the Trionychinae are the
Chitrini, Aspideretini, Trionychini, and Pelodiscini.

TRIBE CHITRINI
(GRAY, 1870; AS CHITRADAE)
NEW RANK

TYPE GENUS: Chitra Gray, 1844.

DIAGNOSIS: Trionychine trionychids in which the foramen posterius canalis carotici interni lies within a ridge extending laterally from the basioccipital tubercle, the eighth cervical has a small ventral keel, and the epipterygoid usually does not contact the palatine but usually does contact the prootic anterior to the foramen nervi trigemini.

CONTENT: In the interest of nomenclatorial stability this tribe is herein considered to be composed of three monotypic genera in two subtribes: Chitra indica, Pelochelys bibroni, and Amyda cartilaginea.

SUBTRIBE CHITRINA
(GRAY, 1870; AS CHITRADAE)
NEW RANK

TYPE GENUS: Chitra Gray, 1844.

DIAGNOSIS: Members of the tribe Chitrini with strong dorsal processes on cervicals four, five, and six, ossifications of the second branchial horn of the hyoid composed of three wide elements which are strongly sutured to one another, jugal always in contact with parietal on skull surface, no dorsal emargination of aperture narium exterum, and vomer dividing maxillae and reaching intermaxillary foramen.

CONTENT: Contains Pelochelys bibroni and Chitra indica and is used to suggest that they share a common ancestor not shared by Amyda cartilaginea.

Chitra Gray, 1844

TYPE SPECIES: Chitra indica (Gray, 1831).

DIAGNOSIS: Members of the subtribe Chitrini in which the anterior edge of the prezygapophysis of the first thoracic vertebra lies at the anterior edge of the carapace, the foramen intermandibularis caudalis is never enclosed by the prearticular, the intermaxillary foramen is quite reduced (about 7% of primary palate), the postorbital bar is two times orbit diameter, the premaxillary is usually absent, and sexual dimorphism may exist (Wirot, 1979).

CONTENT: The only living form is Chitra indica.

Chitra indica (Gray, 1831)

DIAGNOSIS: As for the genus.

Pelochelys Gray, 1864

TYPE SPECIES: Pelochelys bibroni (Owen, 1853).

DIAGNOSIS: Members of the subtribe Chitrini which sometimes have eight neurals (rather than nine, with fused one and two counted as two), vomer often contacts basisphenoid, and the epipterygoids fuse to the pterygoid in adults.

Pelochelys differs further from its living sister taxon, Chitra indica, in retaining primitive features including: prezygapophyses of the first thoracic vertebra recessed below the nuchal, foramen intermandibularis caudalis sometimes enclosed by prearticular, intermaxillary foramen larger (about 37% of primary palate), postorbital bar two-thirds of the width of the orbit, premaxillary usually present, and sexual dimorphism unknown.

SUBTRIBE AMYDINA
(LOVERIDGE, 1942; AS AMYIDAE)
NEW RANK

TYPE GENUS: Amyda Geoffroy, 1809.

DIAGNOSIS: Members of the tribe Chitrini with five plastral callosities, elongate anterior projections of epiplastra, a long symphysis with a strong symphyseal ridge, and frequently a medially constricted basisphenoid.

CONTENT: The only living member is Amyda cartilaginea.

Amyda Geoffroy, 1809

TYPE SPECIES: Amyda cartilaginea (Boddart, 1770).

DIAGNOSIS: As for the subtribe Amydina.

CONTENT: As for the subtribe Amydina.

Amyda cartilaginea (Boddart, 1770)

DIAGNOSIS: As for the subtribe Amydina.
TRIBE TRIONYCHINI
(FITZINGER, 1826; AS TRIONYCHOIDEA)
NEW RANK

TYPE GENUS: Trionyx Geoffroy, 1809.
DIAGNOSIS: Members of the subfamily Trionychinae with eight or fewer neurals (fused first and second count as two), parietal makes up nearly one-quarter of processus trochlearis oticum, and dorsal margin of apertura narium externum is strongly emarginate (except in swinhoei and euphraticus).

CONTENT: Considered to include six living species: triunguis, euphraticus, swinhoei, ferox, spiniferus, and muticus. The relationships within this tribe, as understood from the current analysis, can best be portrayed through the use of two subtribes, three genera, and two subgenera.

SUBTRIBE TRIONYCHINA
(FITZINGER, 1826; AS TRIONYCHOIDEA)
NEW RANK

TYPE GENUS: Trionyx Geoffroy, 1809.
DIAGNOSIS: Members of Trionychini with six ossifications in the corpus hyoidis, epipterygoid fusing to the pterygoid in very large adults, and exoccipital partly or completely isolated from the pterygoid by the basioccipital. Differing further from members of the sister subtribe in its primitive retention of complete eighth pleurals and a smaller intermaxillary foramen (about one-third primary palate).

CONTENT: One species, Trionyx triunguis.

Genus Trionyx Geoffroy, 1809
TYPE SPECIES: Trionyx triunguis (Forskal, 1775).
DIAGNOSIS: As for subtribe Trionychina.
CONTENT: As for subtribe Trionychina.

Trionyx triunguis (Forskal, 1775)
DIAGNOSIS: As for subtribe Trionychina.

SUBTRIBE APALONINA NEW NAME

TYPE GENUS: Apalone Rafinesque, 1832.
DIAGNOSIS: Members of the Tribe Trionychini in which the eighth pair of pleurals is reduced or absent, there are seven or more ossifications in the second branchial horn, the intermaxillary foramen is about 60 percent of primary palate in length, there is no distinct metischial process (except in spiniferus and muticus), and the vomer divides the maxillae and reaches the intermaxillary foramen.

CONTENT: The relationships of the members of this subtribe can be completely portrayed by the use of two generic names, Rafetus and Apalone, with two subgenera (Platypeltis and Apalone) constituting the latter.

Rafetus Gray, 1864

TYPE SPECIES: Rafetus euphraticus (Daudin, 1802).
DIAGNOSIS: Members of the subtribe Apalonina with only two callosities in the plastron, the foramen intermandibularis caudalis never enclosed by the prearticular, and the dorsal edge of the apertura narium externum only weakly emarginate.

CONTENT: Two living species, euphraticus and swinhoei.

Rafetus euphraticus (Daudin, 1802)
DIAGNOSIS: Members of the genus Rafetus with a ventral keel present on the eighth cervical vertebra, the basisphenoid medially constricted in some individuals, and the basisphenoid failing to contact the palatines.

Rafetus swinhoei (Gray, 1873)
DIAGNOSIS: Members of the genus Rafetus in which the jugal contacts the squamosal, the foramen palatinum posterius is surrounded by the palatine, and the basisphenoid contacts the palatines.

Apalone Rafinesque, 1832

TYPE SPECIES: Apalone spiniferus (Le Sueur, 1827).
DIAGNOSIS: Members of the subtribe Apalonina in which the location of the posteriormost neural reversal is highly variable but occurs at or anterior to neural six and in which there is marked sexual dimorphism.

CONTENT: Two subgenera, Apalone and Platypeltis are used within this genus to reflect the relationship of the three included species.
Apalone (Apalone) spinifera
(Le Sueur, 1827)

**Diagnosis:** Members of the genus *Apalone* that can be distinguished from congeners belonging to the subgenus *Platypeltis* by the presence of seven plastral callosities in old adult males, small adult size (200 mm or less disc length), six ossifications in corpus hyoïdis, postorbital bar about one-fifth orbit diameter, metischial process distinct, angle of acromion to scapula approaches that of coracoid to acromion, and contact between pterygoid and foramen nervi trigemini. This species can be distinguished from its sister taxon, *Apalone (Apalone) muticus*, by its higher number of ossifications in the second branchial horn (seven or more), its medially constricted basisphenoid (occurs only in some individuals), and by relatively primitive conditions for nuchal bone (about three times wider than long) and jugal contacts (never contacts parietal on skull surface).

Apalone (Apalone) muticus
Le Sueur, 1827

**Diagnosis:** Members of the genus *Apalone* that can be distinguished from congeners belonging to the subgenus *Platypeltis* by the presence of seven plastral callosities in old adult males, small adult size (200 mm or less disc length), six ossifications in corpus hyoïdis, postorbital bar about one-fifth orbit diameter,metischial process distinct, angle of acromion to scapula approaches that of coracoid to acromion, and contact between pterygoid and foramen nervi trigemini does not occur when epipterygoid is present. This species can be distinguished from its sister taxon, *Apalone (Apalone) muticus*, by its higher number of ossifications in the second branchial horn (seven or more), its medially constricted basisphenoid (occurs only in some individuals), and by relatively primitive conditions for nuchal bone (about three times wider than long) and jugal contacts (never contacts parietal on skull surface).

Apalone (Platypeltis) ferox
(Schneider, 1783)

**Diagnosis:** Members of the genus *Apalone* which can most easily be distinguished from members of the sister taxon (subgenus *Apalone*) by the fusion of the hyo-hypoplastra which occurs in nearly all adults. This species is further diagnosable by only four callosities in the plastron of all adult individuals, eight ossifications in the adult corpus hyoïdis, absence of metischial processes, wider acromion to scapula angle, and large adult size.

TRIBE ASPIDERETINI, NEW NAME

**Type genus:** *Aspideretes* Hay, 1904.

**Diagnosis:** Trionychine turtles with the basisphenoid medially constricted, a strong symphyseal ridge in a depression, the quadrate excluded from the foramen nervi trigemini by contact of the pterygoid and prootic posterior to this structure (except in *A. leithii*), and jugal contacting squamosal in some individuals.

**Content:** Here considered to include two genera, *Aspideretes* and *Nilssonia*.

*Aspideretes* Hay, 1904

**Type species:** *Aspideretes gangeticus* (Cuvier, 1825).

**Diagnosis:** Members of *Aspideretini* most easily recognized by two pairs of neurals between the first pair of pleurals, five callosities in the plastron, and anterior epiplastral projections of intermediate length.

**Content:** The interrelationships of the four living species in this genus is not fully resolved. To reflect this no superspecific ranks are used within the genus. The genus contains four living species: *gangeticus, hurum, leithii*, and *nigricans*.

*Aspideretes gangeticus* (Cuvier, 1825)

**Diagnosis:** A species of the genus *Aspideretes* with seven or more ossifications in the second branchial horn of the hyoid, jugal never contacting parietal on skull surface, and quadrate jugal participating in processus trochlearis oticum.

*Aspideretes hurum* (Gray, 1831)

**Diagnosis:** A species of *Aspideretes* with only one ossification in the second branchial horn, eight ossifications in the corpus hyoïd.
dis, the dorsal margin of the apertura narium externum strongly emarginate, and the epipterygoid (when present) contacting the prootic in front of the foramen nervi trigemini in some individuals.

Aspideretes leithii (Gray, 1872)

**DIAGNOSIS:** Members of *Aspideretes* in which some individuals have eight rather than nine neurals and in which the pterygoid, if contacting the foramen nervi trigemini, does so between the epipterygoid (when present) and the quadrate. Further diagnosed by primitive conditions for those specialized features which are diagnostic for its congeners.

Aspideretes nigricans (Anderson, 1875)

**DIAGNOSIS:** Members of *Aspideretes* in which the jugal never contacts the parietal on the skull surface (true also of *gangeticus*), the foramen posterior canalis carotici interni is located within a crest extending anterolaterally from the basioccipital tubercle, the parietal makes up more than 22 percent of the processus trochlearis oticum, and the epipterygoid is not known to contact the palatine.

Nilssonia Gray, 1872

**TYPE SPECIES:** Nilssonia formosa (Gray, 1869).

**DIAGNOSIS:** Members of Aspideretini with a single neural (fused one and two) between the first pair of pleurals, the nuchal bone only two times wider than long, the last neural reversal occurring at neural seven, the jugal always in contact with the parietal on the skull surface, and the foramen intermandibularis caudalis never enclosed by the prearticular.

**CONTENT:** The single living species *Nilssonia formosa*.

Nilssonia formosa (Gray, 1869)

**DIAGNOSIS:** As for the genus *Nilssonia*.

TRIBE PELODISCINI, NEW NAME

**TYPE GENUS:** Pelodiscus Gray, 1844.

**DIAGNOSIS:** Trionychine turtles in which the epiplastra are significantly anteriorly extended (more than 40% of hyohyoplastron width), the largest adult size is 200 mm or less (with one possible exception), the foramen jugulare posterior is excluded completely or partially from the fenestra postotica by a descending process of the opisthotic, and when the pterygoid contacts the foramen nervi trigemini it does so between the epipterygoid (when present) and the parietal.

**CONTENT:** In order to completely portray relationships and to encourage use of the name *Dogania* for the highly derived species *subplanata*, this tribe is considered to be composed of two subtribes and three monotypic genera.

SUBTRIBE PELODISCINA, NEW NAME

**TYPE GENUS:** Pelodiscus Gray, 1844.

**DIAGNOSIS:** Members of Pelodiscini with seven callosities in the adult plastron, location of the last neural reversal highly variable but always occurring at or anterior to neural six, jugal contacting squamosal in some individuals, and foramen palatinum posterius surrounded by the palatine.

**CONTENT:** Contains only *Pelodiscus sinensis*.

Pelodiscus Gray, 1844

**TYPE SPECIES:** Pelodiscus sinensis (Weigmann, 1835).

**DIAGNOSIS:** Same as for subtribe Pelodiscina.

**CONTENT:** Same as for subtribe Pelodiscina.

Pelodiscus sinensis Weigmann, 1835

**DIAGNOSIS:** Same as for subtribe Pelodiscina.

SUBTRIBE DOGANIINA, NEW NAME

**TYPE GENUS:** Dogania.

**DIAGNOSIS:** Members of the tribe Pelodiscini with four plastral callosities, posteriormost neural reversal occurring as far posterior as neural seven, long anterior processes of the epiplastra, and postorbital bar less than one-fifth of orbit diameter.

**CONTENT:** Two monotypic genera, *Dogania* and *Palea*.
Dogania Gray, 1844

**Type Species:** *Dogania subplana* (Geoffroy, 1809).

**Diagnosis:** Members of the subtribe Doganiina with a complete series of nine neurals (first and second fused) which divide all of the pleurals along the midline, eight ossifications in the corpus hyoidis, basisphenoid often medially constricted, postorbital bar one-ninth of orbit diameter, and maxillae contacting frontals along anterior margin of orbits.

**Content:** Contains only *Dogania subplana*.

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Palea, new genus

**Type Species:** *Palea steindachneri* (Siebenrock, 1906).

**Diagnosis:** Members of the subtribe Doganiina with the nuchal bone only two times wider than long, neural reversal always occurring at the same neural (number 7), jugal always contacting parietal on skull surface, and epipterygoid contacting prootic anterior to the foramen nervi trigemini.

**Etymology:** From the Latin *palea*, meaning wattles, in reference to the autapomorphic structures on the neck.

**Content:** Contains only *Palea steindachneri* (Siebenrock, 1906).

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Appendix 1. Specimens Examined

The modal conditions of characters for members of the Trionychidae listed in tables 3, 11, and 17 are based on the following specimens. For specimens with more than one catalog number (BMNH, MNHNP) the earliest number is given. See acknowledgments for explanation of museum acronyms.

_Apalone ferox_ AMNH 129737, PCHP 343, PCHP 354, PCHP 1171, PCHP 1532, PCHP 1533, PCHP 1534, PCHP unnumbered, UF 10963, UF 11124, UF 11126, UF 14270, UF 14363, UF 18932, UF 32999, UF 33434, UF 33436, UF 33447, UF 33453, UF 37545, UF 40534, UF 52886, UF 52887, UF 53172, UF 53173, UF 53174, UF 53382, UF 53383, UF 53568, UF 53569, UF 53570, UF 53671, UF 53672, UF 53673, UF 54212, UF 54547, UF 5576, UF T-1203.

_Apalone mutica_ PCHP 1611, PCHP unnumbered, UF 55789, UF 57724, UF 57725, UMMZ 128086, UMMZ 155231.

_Apalone spinifera_ IRSNB 231, PCHP 1479, PCHP 1480, PCHP unnumbered, UF 22392, UF 37228, UF 40614, UF 43154, UF 43889, UF 45181, UF 45182, UF 45183, UF 45184, UF 45356, UF 48257, UF 50811, UF 51093, UF 51094, UF 55564.


_Aspideretes gangeticus_ BMNH 48.2.21.41, BMNH 80.1.28, BMNH 86.8.26.1, BMNH 3 unnumbered specimens, EOM 2663, EOM 2664, EOM 2801, MNHNP 1866-151, MNHNP A-5226, MNHNP unnumbered, SMF 52770. _Aspideretes hurum_ BMNH 68.2.12.15, BMNH 86.8.26.2, BMNH 81.7.8.4, BMNH 81.7.8.5, EOM 2681, EOM 2811, EOM 2826, RE 2132, ZSM 26/1912.

Aspideretes leithii BMNH 70.7.11.1, EOM 2627, EOM 2819.

Aspideretes nigricans BMNH 1929.12.23.1, BMNH 1929.12.23.2.

_Chitra indica_ BMNH 47.3.6.21, BMNH 86.2.1.1, BMNH 87.3.30.11, BMNH 1926.12.16.1, BMNH 48.2.1.39, BMNH 1974.2451, BMNH 1984.1276, BMNH unnumbered (mount 220), EOM 2625, EOM 2696, EOM 2699, IRSNB 18.8.88 (?= 3295), MNHNP 180.182, PCHP 1474, PCHP 1707, PCHP 2613, SMF 52768, SMF 52769.

_Cyclanorbis elegans_ BMNH 64.1.25.3, BMNH 64.8.8.9, BMNH 65.5.9.22, BMNH 1900.9.22.8, BMNH 1906.11.16.2, BMNH 1909.10.15.5, BMNH 1949.1.9.58, BMNH 1954.1.14.2, BMNH 1954.1.14.3, BMNH unnumbered, NMW 157, NMW 1436, NMW 1437, NMW 1438, NMW 1439, NMW 1440, NMW 1441, NMW 1504, RMNH 17968, SMF 37475.

_Cyclanorbis senegalensis_ BMNH 63.11.9.6, BMNH 1864.216, BMNH 65.4.6.10, BMNH 65.5.3.72, BMNH 65.5.3.73, BMNH 65.5.3.75, BMNH 65.5.9.19, BMNH 65.5.9.20, BMNH 65.5.9.21, BMNH 1920.1.20.3225, BMNH 1920.1.20.3641, BMNH 1920.1.20.4118, BMNH 1947.3.6.23, BMNH 1949.1.3.57, BMNH unnumbered, MCZ 42599, MNHNP-AC 1944-251, NMW 1257/1, NMW 1257/2, NMW 1434, SMF 37474, ZSM 2509/0.

_Cycloderma aubryi_ BMNH 61.7.29, BMNH 63.6.13.5, FMNH 98752, MCZ 145308, MHNG unnumbered, MNHNP 1889-384, MNHNP 1922-365, MNHNP 1930-362, MNHNP 1944-265,
MNHN-AC unnumbered, MRAC 945, MRAC 2581, MRAC 3050, MRAC 14621, MRAC 14623, MRAC 14662, MRAC 19212, MRAC 19813.

*Cycloderma frenatum* BMNH unnumbered (type of *Aspidochelys livingstoni*), MCZ 50359, NMHM 16692, NMZB 1245, NMZB 6623, SMF 33700, TM unnumbered, UF 52704.

*Dogania subplana* BMNH 53.5.38, BMNH 60.3.19.1045, BMNH 81.10.10.12, BMNH 1929.7.3.10, BMNH unnumbered, MNHNP A5182, MVZ 95937, RMNH unnumbered, UF 56317, USNM 40005, USNM 70835, USNM 222523.

*Lissemys punctata* BMNH 69.8.28.10, BMNH 88.12.3.4, BMNH 1972.2067, BMNH 1972.????, MNHNP A5169, MNHNP-AC 1880-472, NHMG 615.85, NHMG 615.88, NHMG 1557.19, NMW 1872, PCHP 1437, UF 55788, UF 56017, UMMZ 129396, UMMZ 129896, USNM 061903, USNM 061904.

*Nilssonia formosa* BMNH 68.4.3.142, BMNH 81.7.8.3, BMNH 87.3.30.12, BMNH 87.3.30.20, BMNH 91.11.26.6.

*Palea steindachneri* BMNH 1930.4.3.2, MNHNP 1980/1476, MNHNP unnumbered.

*Pelodiscus sinensis* BMNH 62.2.23.9, BMNH 73.7.30.125, BMNH 88.12.3.4, BMNH 1972.2067, BMNH 1972.????, MNHNP A5169, MNHNP-AC 1880-472, NHMG 615.85, NHMG 615.88, NHMG 1557.19, NMW 1872, PCHP 1437, UF 55788, UF 56017, UMMZ 129396, UMMZ 129896, USNM 061903, USNM 061904.


*Trionyx triunguis* BMNH 62.3.20.8, BMNH 65.4.6.9, BMNH 1911.7.27.1, BMNH 1954.1.14.4, IRSNB 3299, KNM ER 8123, KNM 3 unnumbered specimen, MNHNP A5186, MNHNP A5242, MRAC 5446, MRAC 11978, MRAC 12324, MRAC 12329, MRAC 14479, MRAC 15408, MRAC 15651, MRAC 16560, NMW 203, USNM 231704.

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